A B S T R A C T

Title of Document: CAUSES AND CONSEQUENCES OF LONG-DISTANCE DISPERSAL IN A MIGRATORY BIRD, THE AMERICAN REDSTART (*SETOPHAGA RUTICILLA*)

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Long-distance dispersal, the movement of individuals beyond the boundaries of their population for the purpose of breeding, is a central process in ecology and evolution. Unfortunately, the causes and consequences of long-distance dispersal are poorly understood, especially in migratory species due to the difficulty of tracking individuals throughout their annual cycle. Furthermore, although events experienced during one period of the annual cycle can influence the costs of dispersal in subsequent periods, a review of existing literature on dispersal in migratory species indicated that these seasonal interactions have not been widely incorporated into dispersal research. To advance this subject, I used observational and experimental approaches to quantify the causes and consequences of long-distance dispersal in a migratory bird, the American redstart (*Setophaga ruticilla*). Stable hydrogen isotopes from feathers ($\delta^2 H_f$) indicated that yearlings and adults were more likely to disperse north in years with early breeding-season phenology and that yearlings were also more likely to disperse north following winters with

poor habitat conditions in the Caribbean. These results are consistent with the hypotheses that individuals use conditions experienced during migration as a cue for selecting breeding areas. Experimental simulation of social cues further demonstrated that redstarts use both the presence of conspecifics and habitat features to select breeding sites and $\delta^2 H_f$ values of individuals that responded to playback treatments indicated that long-distance dispersers rely more heavily on social cues than local individuals. Reproductive success was not influenced by long-distance dispersal in either sex but male reproductive success was positively correlated with non-breeding territory quality. For adult males, non-breeding territory quality directly influenced the number of young produced. For yearling males, in contrast, high-quality non-breeding territories were associated with higher mating and nesting success but once these differences were accounted for, non-breeding territory quality had no further influence on reproductive success. Collectively, these results suggest that long-distance dispersal may be an effective strategy for responding to advances in breeding-season phenology driven by temperate climate change but that migratory birds may ultimately be limited by the drying in tropical non-breeding areas.

CAUSES AND CONSEQUENCES OF LONG-DISTANCE DISPERSAL IN A MIGRATORY BIRD, THE AMERICAN REDSTART (*SETOPHAGA RUTICILLA*)

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PREFACE

All research was conducted in accordance with permits issued by the U.S. Fish and Wildlife Service, and protocols approved by the Institutional Animal Care and Use Committees of the Smithsonian National Zoological Park, the University of Maryland, and the U.S. Fish and Wildlife Service.

This dissertation was created using the `classicthesis` template developed by André Miede and inspired by Robert Bringhurst's *"The Elements of Typographic Style"*. `classicthesis` is available for both LaTeX and LyX:

`http://code.google.com/p/classicthesis/`

Dedicated to my wife Anya and my sons Jack and 'Man Cub'. Your constant love, patience, and support made this possible.

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OVERVIEW

Long-distance dispersal, defined as the movement of an individual beyond the normal boundaries of its population for the purpose of breeding, is a central process in ecology and evolution. Although long-distance dispersal is generally rare in most species, many ecological and evolutionary processes are sensitive to the rate and magnitude of these movements, including local adaption and speciation, population dynamics, range expansion, and the response of species to climate change. Unfortunately, due to the inherent difficulty of tracking long-distance dispersal, these movements remain poorly understood in most species.

Understanding the causes and consequences of long-distance dispersal is especially difficult in species that migrate annually between distinct breeding and non-breeding grounds due to the scale of these migratory movements and the challenges of tracking individuals throughout their entire annual cycle. Furthermore, there is growing evidence that many life history events, including long-distance dispersal, are shaped by the interaction of events across the annual cycle. These seasonal interactions complicate the study of long-distance dispersal because decisions about where to breed and the reproductive consequences of these decisions may be determined partly by the conditions or events experienced earlier in the year at locations separated by thousands of kilometers.

The primary objective of my dissertation was to quantify how factors occurring throughout the entire annual cycle influence the causes and consequences of long-distance dispersal in migratory species. To set the foundation for the questions addressed by my empirical research, Chapter 2 provides a comprehensive review of the existing research on the proximate factors that influence dispersal in migratory species. Based on this review, I discuss two notable gaps in our current understanding of the causes of dispersal in migratory species. First, very little is known about movements between locations used outside of the breeding season, despite the ecological importance of these movements for individuals and populations. Second, although researchers studying migratory species have realized that events occurring during one period of the annual cycle can interact with events that occur in subsequent periods, these seasonal interactions have not been widely incorporated into dispersal paradigms. I briefly provide a background

on the evidence for seasonal interactions and discuss how seasonal interactions can influence the costs and benefits of dispersal.

The remainder of my dissertation focuses on quantifying the causes and consequences of long-dispersal in a Neotropical migratory bird, the American redstart (*Setophaga ruticilla*). In Chapter 3, I used stable hydrogen isotopes to quantify the rate and direction of long-distance immigration in a population of redstarts and to link these movements to breeding and non-breeding climate conditions and individual traits. Both natal and breeding dispersal were strongly influenced by the timing of breeding-season phenology, with both age classes more likely to disperse north in years with early phenology. Yearlings were also more likely to disperse north following winters with poor environmental conditions in the Caribbean, demonstrating that carry-over effects from the non-breeding season influence natal dispersal in this species. Collectively, these results are consistent with the hypothesis that individuals use phenological cues to select breeding sites and indicate that the timing of migration relative to the phenology of breeding season resources is a principle driver of long-distance dispersal in this species.

Once individuals settle in a breeding area, both philopatric individuals and immigrants are under strong pressure to quickly locate high-quality breeding territories. There is increasing evidence that many animal species use information acquired from conspecifics, termed *social information*, to assess the suitability of potential breeding sites but little is known about the relative importance of different social cues or how the use of social information is modified by long-distance dispersal. In Chapter 4, I used an automated playback experiment to simulate two types of social information, post-breeding *public information* and pre-breeding *location cues*, and determine the relative importance of these cues for breeding site selection by redstarts. In addition, I used stable hydrogen isotopes to determine whether long-distance dispersal influenced the type of information used by individuals that responded to the experimental treatments. Points that received location cue treatments were significantly more likely to be settled by both adults and yearlings than control points that received no playback but we found no evidence that either age class used public information gathered during one season to select breeding sites to following year. Habitat structure also was a strong predictor of settlement probability, indicating that redstarts modified the use of social information based on habitat cues. Furthermore, stable hydrogen isotope signatures from individuals that responded to location cue treatments suggest that long-distance dispersers may rely more heavily on these cues than local recruits. Collectively, these

results indicate that redstarts use multiple sources of information to select breeding sites, which could buffer individuals from selecting suboptimal sites when they breed in unfamiliar locations or when habitat quality becomes decoupled from social cues.

In Chapter 5, I used a combination of stable isotope analysis and Aster life-history models to disentangle the reproductive consequences of long-distance dispersal and non-breeding territory quality. I found no evidence that reproductive success was influenced by long-distance dispersal, suggesting that these movements carry no immediate reproductive costs. Male reproductive success was positively correlated with non-breeding territory quality, although the mechanism of this carry-over effect differed between adults and yearlings. For adult males, non-breeding territory quality directly influenced the number of young produced. For yearling males, in contrast, high-quality non-breeding territories were associated with higher mating and nesting success but once these differences were accounted for, non-breeding territory quality had no further influence on reproductive success. Neither long-distance dispersal nor non-breeding territory quality was found to influence female reproductive success.

As breeding-season phenology in temperate areas has advanced in recent decades, there is concern that some migratory species may not be able to advance their arrival dates on the breeding grounds to keep pace. The results of my dissertation suggest that, rather than adjusting the timing or speed of migration, some individuals may use long-distance dispersal as a mechanism for responding to annual variation in the timing of breeding-season phenology. Once these individuals arrive at a suitable breeding location, they use both social and habitat cues to locate suitable breeding territories and do not appear to suffer reproductive costs associated with these decisions. Collectively, these results suggest that long-distance dispersal may be an effective strategy for coping with the rapid advances in breeding season phenology associated with climate change in temperate areas. However, the tropical non-breeding areas inhabited by American redstarts are predicted to receive less precipitation in the coming decades. Drier conditions will result in lower food resources and delayed departure on spring migration, forcing individuals to disperse farther north to synchronize reproductive efforts with optimal breeding conditions. However, even if individuals are able to locate suitable breeding habitat, the deteriorating conditions in tropical areas will still reduce reproductive output. At present, most assessments of climate change vulnerability focus on the impacts of temperate climate change, but my results underscore the importance of considering how indi-

vidual organisms respond to shifting environmental conditions experienced throughout their entire annual cycle.

2

MOVING BEYOND CONVENTIONAL PARADIGMS TO UNDERSTAND DISPERSAL IN MIGRATORY SPECIES

ABSTRACT

Understanding the factors that influence the costs and benefits of dispersal is a central issue in ecology, evolution and conservation. For species that migrate between distinct breeding and non-breeding grounds, studying dispersal is challenging due to the complexity and scale of their annual movements. Furthermore, the costs or benefits of dispersal in these species may be shaped by the interaction of factors that occur throughout the entire annual cycle. Although recent technological advances have provided a wealth of tools for studying dispersal in migratory species, progress on this subject requires moving beyond conventional paradigms by incorporating our rapidly growing understanding of migratory ecology into dispersal research. Here, we provide a comprehensive review of the existing research on the proximate factors that influence dispersal in migratory species that spans taxonomic groups and periods of the annual cycle. Based on this review, we discuss two notable gaps in our current understanding of the causes of dispersal in migratory species. First, very little is known about movements between locations used outside of the breeding season, despite the ecological importance of these movements for individuals and populations. Second, although researchers studying migratory species have realized that events occurring during one period of the annual cycle can interact with events that occur in subsequent periods, these seasonal interactions have

not been widely incorporated into dispersal paradigms. We briefly provide a background on the evidence for seasonal interactions and discuss how seasonal interactions can influence the costs and benefits of dispersal. Lastly, we suggest important areas for future research.

2.1 INTRODUCTION

Migration, defined as the repeated movement of individuals between distinct breeding and non-breeding areas, is a widespread and common phenomenon across the animal kingdom (Alerstam et al., 2003; Robinson et al., 2009). For all migratory species, whether a salamander moving tens of meters between a breeding pond and terrestrial non-breeding habitat or an Arctic tern flying over 20,000km between Arctic breeding sites and Antarctic feeding grounds, these movements shape every aspect of their ecology and evolution. But while the complexity of migratory movements has long fascinated biologists and non-biologists alike, they also make it difficult to fully understand the life-history of these species. As a result, many basic questions about the ecology of migratory species remain poorly understood (Bolger et al., 2008; Semlitsch, 2008; Faaborg et al., 2010). Addressing these gaps is essential not only for understanding the ecology of migratory species but also for developing effective conservation strategies to manage the multitude of threats facing migratory species across the globe (Wilcove and Wikelski, 2008).

One ecological process that is particularly poorly understood in migratory species is dispersal (Winkler, 2005). To complete their journeys, migratory

individuals rely on a variety of habitats throughout their annual cycle, including breeding and non-breeding sites as well as stopover locations and molting areas (Newton, 2007). At each of these stages, migrants face the choice of whether to return to the location they inhabited the previous year, termed site fidelity (Figure 1a), or to utilize different locations, termed dispersal (Figure 1b-c). For example, an individual returning on spring migration and attempting to breed for the first time could return to its birth place or may instead settle in a new location, resulting in what is commonly referred to as *natal dispersal* (Figure 1b). Likewise, experienced breeders may remain faithful to previous breeding locations or may move to new locations in subsequent years, referred to as *breeding dispersal* (Figure 1b). Collectively, we refer to breeding and natal dispersal as *breeding-season dispersal*. Given the evolutionary and ecological importance of breeding-season dispersal, a large body of theoretical and empirical research has focused on understanding the ultimate and proximate causes of these movements (e.g. Johnson and Gaines, 1990; Bowler and Benton, 2005).

The historical focus of dispersal research on population genetics and gene flow has led to a conventional perspective that equates dispersal with gene flow (e.g. Greenwood, 1980; Johnson and Gaines, 1990). While this definition is widely accepted, ecologists are often interested not in gene flow but in how dispersal influences population dynamics via immigration and emigration (e.g. the 'BIDE' model: Pulliam, 1988; Caswell, 1989). Although the distinction between these two perspectives is generally unnecessary for non-migratory species, many migratory species form distinct populations during both the breeding season and during other periods of the annual cycle (Sweanor and Sandegren, 1989). Because the dynamics of these non-

breeding populations are not directly influenced by reproduction, immigration and emigration are the primary processes driving non-breeding population dynamics (De Los Santos et al., 1986; Berthold and Terrill, 1988), range expansion (Berthold et al., 1992; Hill et al., 1998), and responses to spatial and temporal variation in habitat quality (Hestbeck et al., 1991; Schaefer et al., 2000).

Given the ecological similarity between these non-breeding movements and breeding-season dispersal, we consider them a distinct type of dispersal movement, termed *non-breeding dispersal* (Figure 1c). Although some may take exception to equating these movements within breeding-season dispersal, we argue that the focus on gene flow has biased research against studying ecologically similar movements outside the breeding season, which has hindered understanding the dynamics of non-breeding populations (Sweanor and Sandegren, 1989). Furthermore, because non-breeding dynamics can feedback to influence breeding-season processes (Runge and Marra, 2005), including breeding-season dispersal (Lok et al., 2011), understanding the proximate and ultimate causes of non-breeding dispersal is critical to understanding the ecology and evolution of migratory species.

Regardless of which period of the annual cycle it occurs, understanding the causes and consequences of dispersal is central to understanding the ecology, evolution and conservation of migratory species (Faaborg et al., 2010; Clobert et al., 2012). Unfortunately, dispersal and migration have traditionally been relegated to separate literatures (Nathan et al., 2008) and there has been little research on how the migratory annual cycle shapes dispersal in these species (Winkler, 2005). Although several studies have tested whether migration per se influences dispersal distance (Paradis et al., 1998;

Sutherland et al., 2000), these studies were restricted to birds and the comparative approach used by these studies provides little mechanistic insight into the forces shaping dispersal in migratory species (Bowler and Benton, 2005). In reality, the costs or benefits of dispersal shaped by complex trade-offs imposed by each species' unique life-history (Bonte et al., 2012) and progress on this important subject requires moving beyond conventional dispersal paradigms and towards a mechanistic approach that explicitly considers how the costs or benefits of dispersal are shaped by migration.

One of the major obstacles to developing a general understanding of the interaction between migration and dispersal is that the relevant studies are largely divided into non-overlapping, taxon-specific literatures (Nathan et al., 2008). To this end, the primary purpose of this contribution is to review and synthesize the existing literature on the causes of dispersal in migratory species at each stage of the annual cycle. Based on this review, we then identify and discuss two major gaps in our understanding of dispersal in migratory species. First, because dispersal research has mainly focused on breeding-season dispersal, dispersal outside of the breeding season is poorly understood. Second, few studies have considered how events occurring throughout the annual cycle interact to influence the costs or benefits of dispersal. Given the increasing evidence that life-history traits of migratory species are shaped by seasonal interactions (Marra et al., 2006), we discuss how this within-season bias is a major impediment to understanding dispersal in migratory species and highlight important areas for future research. It is our hope that the ideas proposed here will stimulate novel hypotheses and innovative solutions to advance future research on dispersal in migratory species.

2.2 LITERATURE REVIEW

Conducting a comprehensive literature review on dispersal in migratory species is challenging. First, migratory species show a wide diversity of life-history traits and annual schedules. For some taxa, like many passerine birds, all reproductive activities (e.g. pair formation, mating, nesting) occur annually at one location and once completed, individuals migrate to non-breeding sites for the remainder of the year (but see Rohwer et al., 2009). Other species, however, carry out reproductive activities at a number of locations throughout the annual cycle. Many ducks and geese, for example, form pair bonds during the winter prior to migrating together to breeding grounds (Robertson and Cooke, 1999) and many ungulates migrate as herds to traditional mating grounds before moving to separate calving grounds for the remainder of the year (Danell, 2006). For other species, migratory movements take place over a number of years or generations. Sea turtles, for example, spend several years on communal feeding grounds before returning to their nesting beaches to reproduce (Lutz et al., 2003) and one generation of monarch butterflies makes the southbound migration each fall while three generations make the return the trip in the spring (Malcolm et al., 1993). As a result of these life-history variations, generalizing movements and periods of the annual cycle across taxa can be complex (Nathan et al., 2008).

In addition, the terminology used to describe types of movement is often highly variable across taxa. Movements that have the same biological outcome may be termed *dispersal* when applied to birds (Greenwood and Harvey, 1982), *straying* in the case of fish (Quinn et al., 1991), or *ranging*

in regards to ungulates (Thirgood et al., 2004). To make matters worse, the term migration is often used synonymously with dispersal (e.g. Johnson and Gaines, 1990). Lastly, it is likely that the published literature on dispersal is biased towards positive results (Csada et al., 1996), making it difficult to assess the generality of certain results.

For this review, we searched existing literature on dispersal in migratory species by searching the ISI Web of Science database and Google Scholar using the term "migratory" plus terms related to dispersal (e.g. dispersal, natal dispersal, breeding dispersal, site fidelity, philopatry, straying, natal homing). We also conducted secondary searches using the same dispersal terms plus key taxonomic groups known to show migratory behavior (e.g. birds, ungulates, whales, sea turtles, salamanders, fish). Finally, we reviewed the references in key publications located from these searches to identify other relevant studies.

We included in the review any study that directly or indirectly quantified *proximate* factors influencing intra-specific variation in dispersal in a species or population of migratory individuals. Unfortunately, due to the logistical difficulty associated with directly tracking dispersal events, the majority of studies focused on indirect measures of dispersal, including genetic variation or rates of site fidelity. Although we acknowledge the limitations of making inferences about dispersal from indirect methods (Clobert et al., 2001), these studies provide the majority of, and in some cases the only, information about dispersal during certain periods or for some taxa. Therefore, including these studies was necessary to identify general patterns and research needs. Studies that simply report rates of site fidelity or gene flow without relating the patterns to some proximate factor (e.g. age, sex, den-

sity) were not included. In addition, because our interest was in the causes of intra-specific variation in dispersal, we did not include studies focused on comparing inter-specific patterns of dispersal (e.g. Paradis et al., 1998; Møller et al., 2004).

After compiling publications that matched our search criteria, we divided studies based on the period of the annual cycle during which dispersal or site fidelity was studied (i.e. breeding, non-breeding, stopover or molt). As discussed above, variation in life-history strategies made it difficult to unequivocally categorize periods of the annual cycle for all taxa. Nevertheless, we defined "breeding season" as the period during which the majority of reproductive activity (e.g. nesting, birthing) takes place, though we acknowledge that in some cases important breeding activities may take place during other periods. "Non-breeding" was defined as the stationary period that does not serve as the primary reproductive period. Our definition of dispersal also includes between-year movements of individuals between sites during other periods of the annual cycle. Therefore, we also included studies investigating factors that influence dispersal between stopover locations used on successive migrations and, for birds, dispersal between locations used for molting.

Results of Literature Review

Breeding Season

Not surprisingly, the majority ($\sim 70\%$; Figure 2) of research on dispersal in migratory species has been focused on the breeding season (i.e. natal and

breeding dispersal; Table A1a). Although our review cover a wide range of species, study designs and spatial scales, a number of general patterns emerge. Natal dispersal appears to occur more often and over larger distances than breeding dispersal in most species, particularly birds (Shields, 1984; Hansson et al., 2002; Sedgwick and Grubb Jr, 2004; Hosner and Winkler, 2007; Calabuig et al., 2008; Briggs et al., 2012) and amphibians (Berven and Grudzien, 1990; Gamble et al., 2007). However, this was not always the case, particularly in studies of mammals (e.g. Schaefer et al., 2000; Deutsch et al., 2003). Second, patterns of sex-biased dispersal in migratory species are generally consistent with those of non-migratory species (Greenwood 1980). In most birds, females exhibit lower site fidelity (e.g. Murphy, 1996; Linkhart et al., 2007) are more likely to disperse (e.g. Winkler et al., 2004; Calabuig et al., 2008) and disperse farther than males (e.g. Pärt, 1990; Forero et al., 2002; Winkler et al., 2005; Briggs et al., 2012), although waterfowl that mate during the winter show the opposite patterns (e.g. Robertson and Cooke, 1999; Nicolai et al., 2005; Phillips and Powell, 2006). Most migratory mammals exhibit male-biased dispersal (e.g. Brown, 1992; Engelhaupt et al., 2009). Dispersal also tended to be male-biased in migratory fish (Neville et al., 2006; Hamann and Kennedy, 2012) and reptiles (Karl et al., 1992; Velez-Zuazo et al., 2008) but little evidence for sex-biased dispersal exists for migratory amphibians (Trenham et al., 2001).

Another factor consistently found to influence site fidelity and dispersal during the breeding period was reproductive performance. Particularly in birds (Oring and Lank, 1982; Shields, 1984; Pärt and Gustafsson, 1989; Murphy, 1996; Beheler et al., 2003; Linkhart et al., 2007), individuals of both sexes were more likely to disperse after poor reproductive performance

than individuals that reproduced successfully, while in mammals limited evidence suggests it was the successful individuals that were often more likely to disperse the following year (caribou: Schaefer et al., 2000). There is also substantial evidence that individuals of many migratory species prospect the territories of conspecifics to gain information about territory quality (reviewed by Reed et al., 1999) but few studies have directly linked prospecting behavior to subsequent dispersal decisions (Forero et al., 2002; Pärt and Doligez, 2003). Collectively, the patterns of age-, sex-, and reproductive-biased dispersal observed in migratory species suggest that the ultimate causes of dispersal in these species may be similar to those shaping dispersal in closely-related non-migratory species.

Aside from age, sex and reproductive performance, few factors appear to influence breeding-season dispersal consistently across species. For example, studies investigating the role of body size on breeding-season dispersal in migratory birds have found evidence for both a positive (van der Jeugd, 2001) and a negative relationship (Nilsson, 1989) and many other studies have found no relationship (Pärt, 1990; Brown and Brown, 1992; Forero et al., 2002; Briggs et al., 2012). We did not identify any studies investigating the role of body size on breeding-season dispersal in non-avian migratory species. Similar ambiguity exists regarding the role of other factors, including body condition (Pärt, 1990; Forero et al., 2002; Calabuig et al., 2008), population density (Forero et al., 2002; Gamble et al., 2007; Hamann and Kennedy, 2012), and patch quality (van der Jeugd, 2001; Briggs et al., 2012). Parasitism has been implicated as an important driver of breeding-season dispersal in migratory and non-migratory species (Møller et al., 2004) but we found only one study directly linking parasitism to intra-specific vari-

ation in breeding-season dispersal behavior in a migratory species (Brown and Brown, 1992). Thus, while breeding-season dispersal has been relatively well-studied in migratory species, researchers still have only a rudimentary understanding of the proximate drivers of natal and breeding dispersal.

Non-breeding season

For many migratory species, the non-breeding period represents the largest portion of the annual cycle and during this period individuals must locate habitat suitable for survival (Dugger et al., 2004; Johnson et al., 2006) and for preparing for subsequent migration and breeding attempts (Marra et al., 1998). To accomplish these goals, individuals may return to locations used the previous year or they may choose to change locations, a process we refer to as non-breeding dispersal (Figure 1c). As with breeding-season dispersal, non-breeding dispersal shapes the dynamics of non-breeding populations and can also carry over to influence a number of population-level processes during the breeding season (Sutherland, 1996; Runge and Marra, 2005). Despite the importance of these movements, only 23% of studies identified by our review focused on non-breeding dispersal (Figure 2; Table A1b) and most of these have focused on birds and mammals.

During the non-breeding period, migratory species display a continuum of movement types, from largely nomadic (Mueller et al., 2011) to highly faithful to specific territories (Hestbeck et al., 1991; Holmes and Sherry, 1992). As during the breeding season, these movement types are largely driven by spatio-temporal variation in resource quality and predictability (Mueller and Fagan, 2008). For example, species that rely on resources that vary unpredictably within the non-breeding period are generally nomadic

during this period (Pearson, 1980; Terrill, 1990; Renfrew et al., 2013) and fidelity to non-breeding locations both within and among years is generally very low. In other cases, resources may be largely stable within years but may vary unpredictably across years and this pattern appears to select for high within-season fidelity but low between-year fidelity (birds: Diefenbach et al. 1988; Hestbeck et al. 1991; mammals: Brown 1992; Wittmer et al. 2006). Species that use resources that are stable and predictable across years generally remain faithful to specific non-breeding territories within and between seasons (birds: Wilson et al., 1991; Holmes and Sherry, 1992). However, even in these species, some individuals do disperse between years (e.g. Brown, 1992; Lok et al., 2011), suggesting that factors other than spatio-temporal resource dynamics also influence non-breeding dispersal.

Aside from variation in habitat quality, however, few general patterns are apparent from the studies that have focused on non-breeding dispersal. For example, although non-breeding site fidelity appears to increase with age in birds (Wilson et al., 1991; Latta and Faaborg, 2001; Marchi et al., 2010; Lok et al., 2011) and mammals (Schaefer et al., 2000), this was not true in all cases (Holmes and Sherry, 1992; Deutsch et al., 2003). In contrast to breeding-season dispersal, little evidence exists for consistent sex-biased dispersal during the non-breeding period in birds(Holmes and Sherry, 1992; Reed et al., 1998; Bassett and Cubie, 2009), mammals (Brown, 1992; Deutsch et al., 2003), or amphibians (Dole and Durant, 1974). In the few cases where estimates of site fidelity or dispersal are available for the same species during both the breeding and non-breeding seasons, results are conflicting. For example, Holmes and Sherry (1992) found that site fidelity in two warbler species was higher during the non-breeding period

than during the breeding period. In contrast, female mule deer dispersed shorter distances between consecutive summer ranges than between consecutive winter ranges, while dispersal distances in males did not differ between seasons (Brown, 1992).

The lack of general patterns identified by our review is likely due in part to the relatively small number of studies focused on the non-breeding period and the fact that very few studies have directly measured non-breeding dispersal (Hestbeck et al., 1991; Wilson et al., 1991; Brown, 1992; Holmes and Sherry, 1992; Lok et al., 2011). Given the critical importance of the non-breeding period to migratory species, it is clear that much more research on non-breeding dispersal is needed and as tracking technologies continue to improve, this should be a high priority for future research.

Migration

Individuals of all migratory species rely on a number of temporary sites during other periods of the year to successfully complete their annual cycles. For example, many migrants, including birds (Newton, 2007), marine mammals (Deutsch et al., 2003), terrestrial mammals (Bartlam-Brooks et al., 2011), bats (McGuire et al., 2012), and amphibians (Baldwin et al., 2006), require patches of suitable habitat to rest and refuel during migration. Furthermore, many species rely on stopover locations that are either ephemeral in nature (Baldwin et al., 2006; Warnock and Bishop, 1998) or that are being increasingly degraded by anthropogenic modifications (Baker and Rao, 2004; Wilcove and Wikelski, 2008). As a result, understanding the factors that influence the dispersal of individuals between stopover habitats used

in successive years is critical to developing effective conservation strategies for migratory species (Catry et al., 2004; Sheehy et al., 2011).

However, very few studies have focused on the causes of fidelity to migratory stopover locations and we did not identify any studies focused on non-avian species (Figure 2; Table A1c). The lack of research on dispersal during the migratory period is no doubt a reflection of the difficulty associated with tracking individuals during the migratory period. Nevertheless, several studies have quantified rates of site fidelity to migratory stopover locations in birds (e.g. Cantos and Tellería, 1994; Catry et al., 2004; Yohannes et al., 2007) and advances in tracking technology have given researchers the ability to track the migratory routes of individual organisms over multiple years (e.g. Meyburg et al., 2003; Broderick et al., 2007; Stanley et al., 2012). Continued application of these technologies has potential to uncover important information about how and why individuals choose particular staging or stopover locations during migration and this information is critically needed to effectively protect key habitats along migration routes (Sheehy et al., 2011).

Molt

For migratory birds, molting is an important event in the annual cycle and many species have developed complex movement patterns to ensure that this energetically expensive process takes place at locations with adequate resources (Newton, 2007). Thus, understanding how individuals locate and utilize locations for molting is critical to understanding the ecology and conservation of these species. As with dispersal between stopover sites, there have been very few studies on dispersal between locations used for molting

in successive years (Figure 2; Table A1d), making any general conclusions about dispersal during this period impossible.

Conclusions of Literature Review

The studies identified in Table A1 represent the most extensive review on proximate causes of dispersal in migratory species to date and highlight a number of important gaps in our understanding of dispersal in migratory species.

Moving dispersal research beyond the breeding season

The overwhelming majority of research on dispersal in migratory species has focused on the breeding season (Figure 2; Table A1). Given the historic focus of dispersal research on gene flow (Johnson and Gaines, 1990), this bias is perhaps unsurprising. However, dispersal between locations used during other periods of the year share many of the same ecological consequences as breeding-season dispersal and understanding the causes of these movements is critical to understanding the dynamics of non-breeding populations and to predicting how species will respond to environmental changes. Unfortunately, little is known about the causes of dispersal outside of the breeding season, particularly the factors that influence whether individuals use different stopover or molting locations between years. Expanding the scope of dispersal research to include these periods should be a high priority for future research.

Within-season bias

A less obvious, but no less important, characteristic of the studies reviewed here is that virtually all focused exclusively on the role of factors occurring within the same period as dispersal. For example, with the exception of three studies (Møller et al., 2006; Studds et al., 2008; Cherry et al., 2013), all research on the causes of natal or breeding dispersal consider only factors experienced during the breeding season. In effect, this within-season bias implicitly treats the phases of the annual cycle as discrete periods within which life-history events are independent of events that occur during other periods. But this approach is fundamentally inconsistent with the biology of these species (Norris and Marra, 2007). In migratory species, there is growing evidence that events occurring throughout the entire annual cycle interact (Marra et al., 2006)and these seasonal interactions have important implications for understanding dispersal. Given the myriad of ways these seasonal interactions shape other important life-history events (see below), moving beyond this within-season bias is essential to developing a mechanistic understanding of dispersal in migratory species.

2.3 A NEW FRONTIER: CARRY-OVER EFFECTS AND DISPERSAL

Seasonal interactions and the life-history of migratory species

There is a growing recognition amongst scientists studying migratory species that the periods of the annual cycle are inextricably linked, such that ecological events within one season influence events in subsequent seasons. These

ecological connections are called "seasonal interactions" and can occur at both the population and the individual levels (Runge and Marra, 2005; Marra et al., 2006). At the population level, seasonal interactions operate primarily through density-dependent feedbacks between different periods of the annual cycle (Runge and Marra, 2005). At the individual level, seasonal interactions are referred to as carry-over effects and occur when events or conditions experienced during one period determine the timing or condition of individuals transitioning between periods. As a result, these non-fatal residual effects influence ecological processes during subsequent seasons (Runge and Marra, 2005).

Over the past several decades, evidence that carry-over effects are a widespread and important phenomenon has grown rapidly (Webster et al., 2002; Norris and Marra, 2007; Harrison et al., 2011). To date, most research on carry-over effects has focused on how non-breeding season events influence subsequent reproductive success. For example, American redstarts (*Setophaga ruticilla*) that occupy high-quality territories depart earlier on spring migration, arrive earlier on the breeding grounds, and have higher reproductive success than individuals from low-quality habitat (Marra et al., 1998; Studds and Marra, 2005; Reudink et al., 2009a). Additional evidence that carry-over effects from the non-breeding period are important drivers of reproductive success in migratory species has been found in other bird species (Legagneux et al., 2012; Rockwell et al., 2012), mammals (Perryman et al., 2002; Cook et al., 2004), reptiles (Broderick et al., 2001), fish (Kennedy et al., 2008), and invertebrates (Olive et al., 1997). There is also growing evidence, mainly from birds, that carry-over effects influence other ecological processes, including the timing of molt and migration (Stutchbury

et al., 2011; Mitchell et al., 2012), the distribution of individuals during the non-breeding season (Bogdanova et al., 2011; Catry et al., 2013) and the body condition of individuals prior to fall migration (Mitchell et al., 2011). Taken together, these studies confirm that carry-over effects are a pervasive phenomenon and demonstrate that the life-history of migratory species cannot be understood without an explicit focus on the entire annual cycle (Marra et al., 2006).

Carry-over effects and the costs and benefits of dispersal

As with other life-history events, dispersal behaviors are the result of complex cost-benefit trade-offs that are shaped by many factors, including phenotypic traits, social status, environmental conditions, and trade-offs between life-history events (Bowler and Benton, 2005; Bonte et al., 2012; Matthysen, 2012), many of which are sensitive to carry-over effects from preceding periods (Harrison et al., 2011). Although there are potentially many ways for carry-over effects to influence dispersal dynamics, we focus our discussion on the role of three factors that are known to influence dispersal and are known to be sensitive to carry-over effects: temporal variability in habitat quality, body condition, and trade-offs between life-history events (Figure 3).

Many environments are characterized by predictable spatio-temporal variation in habitat quality (Alerstam et al., 2003) and in response to this variation, migratory species have evolved complex movement strategies to ensure that life-history events coincide with brief but intense peaks in re-

source abundance (Mueller et al., 2011). However, even in habitats with predictable variation in resource abundance, the phenology of resource peaks can vary substantially and unpredictably between years (Townsend et al., 2013). High temporal variation in habitat quality is known to select for flexible dispersal strategies (McPeek and Holt, 1992; Mueller et al., 2011) and indeed, many migratory species are known to track resource phenology as they migrate (Hestbeck et al., 1991; van der Graaf et al., 2006; Bischof et al., 2012; Husek et al., 2014), thereby ensuring that life-history events are synchronized with optimal conditions.

However, the fitness of migratory species is influenced not by the absolute timing of resource phenology but instead by the timing of resource phenology *relative* to the timing of life-history events. Because the timing of migration is often influenced by conditions experienced during the preceding period of the annual cycle (Studds and Marra, 2011; Stutchbury et al., 2011), carry-over effects may interact with spatio-temporal variation in resource phenology to influence the costs or benefits of dispersal. An individual that migrates early, for example due to favorable non-breeding conditions, will experience very different dispersal costs than an individual migrating later because each individual will move across distinct phenological landscapes. Consistent with this hypothesis, Studds et al. (2008) found that American redstarts that held high-quality territories during their first winter on average departed early on spring migration and dispersed south of their natal latitude whereas individuals from low-quality habitat on average departed later and dispersed north (Studds et al., 2008). Carry-over effects are known to have a strong influence on the timing of migration in other

species as well (Harrison et al., 2011) and therefore may be a pervasive force shaping dispersal costs in migratory species (Figure 3).

Empirical and theoretical studies have also demonstrated that body condition can have a strong influence on the costs of dispersal (Ims and Hjermann, 2001; Kisdi et al., 2012), though the relationship between dispersal propensity and body condition may be positive or negative depending on the mortality risks of dispersal and spatio-temporal variation in habitat quality (Bonte and de la Pena, 2009; Gyllenberg et al., 2011). In addition, numerous studies have shown that the body condition of migratory individuals transitioning between periods of the annual cycle is strongly influenced by conditions experienced during the preceding period (Harrison et al., 2011), suggesting that carry-over effects may also play an important role in shaping body condition-dependent dispersal costs (Figure 3). Indeed, Møller et al. (2006) demonstrated that Arctic terns (*Sterna paradisaea*) transition into the breeding period in poor body condition following winters with high sea surface temperatures and low krill abundance in the region where this species spends the non-breeding period, which in turn increased the costs of breeding dispersal and reduced dispersal distance (Møller et al., 2006). These results provide empirical evidence that carry-over effects can influence dispersal via their impacts on body condition and suggest that these effects may be an under-appreciated force shaping the costs of dispersal in migratory species.

Finally, there is widespread evidence that trade-offs between life-history events influence the costs of dispersal (Bonte et al., 2012) as well as many aspects of migration, including arrival date on the breeding grounds (Kokko, 1999), migration speed and fuel loads carried during migration (Alerstam,

2011), stopover and molting site selection (Ydenberg et al., 2002; Ebbinge et al., 2013), and avoiding predation (Hebblewhite and Merrill, 2009). Thus, it is likely that trade-offs imposed by migration may also influence dispersal in migratory species. For example, Cherry et al. (2013) found the breeding dispersal of migratory polar bears (*Ursus maritimus*) is partly determined by a trade-off between the benefits of accumulating fat reserves prior to migrating to terrestrial breeding areas versus the costs of dispersing to unfamiliar breeding sites. Similarly, Ebbinge et al. (2013) found that fidelity to molting sites used by Black-bellied brent geese (*Branta b. bernicla*) is driven by a trade-off between maximizing fledglings survival versus selecting the highest quality molting sites for adults.

These studies demonstrate a number of ways that events or conditions experienced during one period of the annual cycle can carry-over to influence the costs or benefits of dispersal during subsequent periods. Of course, there are many other ways that carry-over effects may influence dispersal in migratory species. For example, age-specific migration patterns occur in many species when older individuals dominate non-breeding sites closest to breeding sites, thereby forcing subordinates to migrate further and spend the non-breeding period in sub-optimal sites (Ketterson and Nolan, 1983). Because competitive status and migration costs change throughout an individual's lifetime, subordinate individuals may shift non-breeding locations as they grow and gain competitive advantages, which could explain the age-biases in non-breeding site fidelity observed in some migratory species (Wilson et al., 1991; Schaefer et al., 2000; Latta and Faaborg, 2001). Although much more work is needed on this subject, the growing number of empirical examples demonstrate that considering the role of carry-over ef-

fects is necessary to developing a mechanistic understanding of the costs and benefits of dispersal in migratory species. Fortunately, the increasing number of analytical and technological tools for studying dispersal provide exciting opportunities to make progress on this subject.

2.4 FUTURE DIRECTIONS

Advancing our understanding of the interaction between migration and dispersal requires moving beyond the constraints of conventional dispersal paradigms. Progress on understanding dispersal in migratory species will require novel approaches that synthesize research and techniques from across disciplines and taxa to find innovative methods for studying dispersal in the field. More importantly, progress will require adopting a "full annual cycle" perspective of dispersal. This perspective must recognize: 1) that dispersal is an ecological process that can occur at each stage of the annual cycle; and 2) the costs and benefits of dispersal can be influenced by factors occurring throughout the entire year and be the result of seasonal interactions. In the following section, we highlight a number of other areas that we believe will be particularly fruitful for future research.

Carry-over effects and the fitness consequences of dispersal

Understanding the relationship between dispersal and fitness is central to understanding the ecological and evolutionary consequences of dispersal (Doligez and Pärt, 2008). In migratory species, disentangling the fitness

consequences of dispersal is challenging because survival and reproductive success are influenced by a number of factors other than dispersal, including arrival date (Kokko, 1999), carry-over effects from the non-breeding season (Marra et al., 1998), and even large-scale climate events (McKellar et al., 2012; Rockwell et al., 2012). As a result, accurately quantifying the fitness consequences of dispersal requires accounting for the influence of these factors. In addition, because dispersal may be a strategy for managing the trade-offs associated with migration, the fitness consequences of dispersal may not be consistent across space or time and may differ among individuals. Unfortunately, previous research on the consequences of dispersal in migratory species has not considered these complications (Pärt, 1990; Hansson et al., 2004). Future researchers should be aware of these complicating factors and carefully design studies to isolate the role of dispersal.

The need for theory

One notable result of our literature review was that we found no theoretical studies exploring the relationship between migration and dispersal. Although the theoretical literature on dispersal is substantial, the lack of work on the role of migration is perhaps unsurprising. Only recently have there been attempts to understand how dispersal is influenced by movements that do not function primarily to locate and colonize new habitat, including foraging, mate finding or avoiding predation (e.g. van Dyck and Baguette, 2005; Stevens et al., 2012). However, incorporating these "routine" movements into theoretical research on dispersal has proved valuable for de-

veloping mechanistic models of dispersal and for understanding how changes to the landscape influence dispersal behavior in butterflies (van Dyck and Baguette, 2005). Because tracking dispersal in wild populations will remain an obstacle to empirical advances, expanding the scope of these theoretical studies to include migration will be an important step for making progress on this subject.

Several existing modeling frameworks could be modified to explore dispersal dynamics in migratory species (Alerstam, 2011). For example, integrating dispersal into optimal migration models could be a fruitful approach for understanding how the constraints imposed by migration influence dispersal. Game theory (Kokko, 1999) and annual routine models (Hedenstrom et al., 2007) are ideally suited to modeling processes that involve multiple trade-offs and could easily be modified to include dispersal as a strategy for optimizing time, energy or survival constraints during migration.

Existing dispersal models can also provide a framework for incorporating dispersal behaviors into optimal migration models. For example, a number of models have been developed to explore how search costs and settlement rules influence patterns of dispersal (Baker and Rao, 2004; Stamps et al., 2005) and these models could be modified to fit within existing migration models. Additionally, existing models that explore how search and settlement decisions are influenced by body condition (Kisdi et al., 2012), timing (Stamps et al., 2005), spatio-temporal variation in habitat quality (Dytham and Travis, 2012), and social information (Doligez et al., 2003) could be particularly well-suited for integrating the role of carry-over effects from preceding periods of the annual cycle. In general, however, many of these modeling frameworks have been developed for species with annual life-cycles

and more work is need to develop models that accommodate more complex life-histories such as migration (Kokko, 1999). Finally, given the complexity of factors influencing individual dispersal decisions, agent-based models could be useful for exploring the interactions between various biotic and abiotic factors thought to influence dispersal (Murrell et al., 2002; Mueller and Fagan, 2008; Travis et al., 2012), particularly for species that have been well studied throughout their entire annual cycle.

The importance of scale

The issue of scale is a critical component of all dispersal research. From a logistical standpoint, the scale at which studies are conducted can introduce important biases (Baker et al., 1995; Koenig et al., 1996) and can influence the interpretation of data (Robertson and Cooke, 1999). From a biological standpoint, the factors that influence dispersal at one scale (e.g. short-distance dispersal) may differ from the factors that influence dispersal at other scale (e.g. long-distance dispersal: Ronce, 2007).

To date, most research on the causes of dispersal in migratory species has taken place over relatively small areas (Pärt, 1990; Morton, 1992; Briggs et al., 2012). In contrast, many of the mechanisms related to carry-over effects operate over relatively large scales. For example, poor quality non-breeding habitat can force individuals to delay spring migration by up to a week (Studds and Marra, 2011), during which time phenological advances on the breeding ground will shift substantially north. If individuals use phenological cues to select breeding sites, than such delays will result in

dispersal distances on the order of hundreds of kilometers (Studds et al., 2008). Therefore, a mechanistic understanding of how selective pressures on dispersal vary across scales in migratory species will require expanding empirical studies to include long-distance dispersal movements.

Dispersal and migratory connectivity

In addition to an increased focus on long-distance dispersal, future research on dispersal in migratory species will benefit from considering the degree to which individuals from one breeding (or non-breeding) population migrate to the same non-breeding (or breeding) location, referred to as migratory connectivity. Migratory connectivity is central to the ecology and evolution of migratory species, influencing population dynamics, local adaptation, and the strength of carry-over effects because individuals inhabiting different parts of the breeding or non-breeding ranges experience different climate and weather patterns and differ in the timing and distance of migration (Webster et al., 2002; Marra et al., 2006). If these factors influence dispersal, than understanding connectivity is critical to understanding how factors occurring throughout the annual cycle influence dispersal. Unfortunately, patterns of connectivity have not been quantified for most migratory species (Marra et al., 2006), making advances on this subject important for understanding dispersal in migratory species.

Fortunately, recent technological advances have provided new tools for studying long-distance dispersal and migratory connectivity. For example, stable isotopes, particularly hydrogen, have proven useful for detecting large-

scale dispersal events (Hobson et al., 2004; Studds et al., 2012; van Wilgenburg et al., 2012) and genetic methods also show promise in some cases (Hansson et al., 2002; Ekblom and Galindo, 2010). Combining these approaches with tools that have been developed for studying carry-over effects, including stable isotopes (Marra et al., 1998), light-level geolocators (Bogdanova et al., 2011), and direct tracking methods such as satellite tags (Zbinden et al., 2011), will be particularly useful for connecting dispersal to events occurring throughout the entire annual cycle. Future advances in our ability to track individuals continuously throughout the year (Wikelski et al., 2007) and across years, will revolutionize our ability to answer these questions.

Non-migratory species

Although the focus of this review has been on dispersal in migratory species, it is important to note that carry-over effects operate in non-migratory species as well (Harrison et al., 2011; Plummer et al., 2013) and have potential to influence dispersal in these species. For example, (Nilsson and Smith, 1988) found that juvenile Marsh tits (*Parus palustris*) from early broods were more likely to become established in high-quality sites during their first winter than individuals from later broods. Furthermore, the individuals that wintered in high-quality sites had higher annual survival and were more likely to breed in the high-quality sites in subsequent years than the later-hatching juveniles that were forced into marginal non-breeding habitat. This study provides an excellent example of how consideration of

carry-over effects and a "full annual cycle" perspective are necessary for a mechanistic understanding of dispersal and underscores the importance of these ideas for migratory and non-migratory species alike.

2.5 CONCLUSIONS

Our review provides a comprehensive summary of existing research on dispersal in migratory species and makes clear that dispersal remains a poorly understood process in these species. While a number of factors, particularly the difficulty associated with tracking migratory individuals, have hindered previous research, adherence to conventional dispersal paradigms remains a major obstacle to developing a mechanistic understanding of dispersal in migratory species. Fortunately, recent advances in our ability to track migratory individuals throughout the annual cycle, combined with a growing recognition of the importance of seasonal interactions, provide scientists with unprecedented abilities to understand dispersal in migratory species. Still, while these advances have tremendous potential for advancing this subject, they will only prove useful if researchers overcome the traditional barriers imposed by sub-disciplines, taxonomic groups and geographical borders and move towards a mechanistic perspective focused on how the costs and benefits of dispersal are shaped by factors occurring throughout the entire annual cycle.

Furthermore, migratory species across the planet face a growing number of anthropogenic threats that are altering the location or quality of habitats used throughout their annual cycle (Wilcove and Wikelski, 2008).

Rapid degradation of breeding habitats, non-breeding habitats and critical stopover locations have already led to significant declines of many species (Sutherland, 1996; Bolger et al., 2008; Wilcove and Wikelski, 2008) and climate change in both temperate and tropical regions is resulting in large-scale changes to the distribution and quality of remaining habitats (Neelin et al., 2006; Both et al., 2010; Knudsen et al., 2011). Whether or not species are able to respond to these changes depends in large part on the flexibility of dispersal behaviors (Clobert et al., 2012), but as we have outlined here, it is likely that destruction or degradation of habitats used during one phase of the annual cycle will carry-over to influence the ability of species to respond to changes during subsequent periods. Consequently, a 'full life-cycle' perspective of both dispersal and conservation of migratory species will be critical to developing effective conservation measures for migratory species.

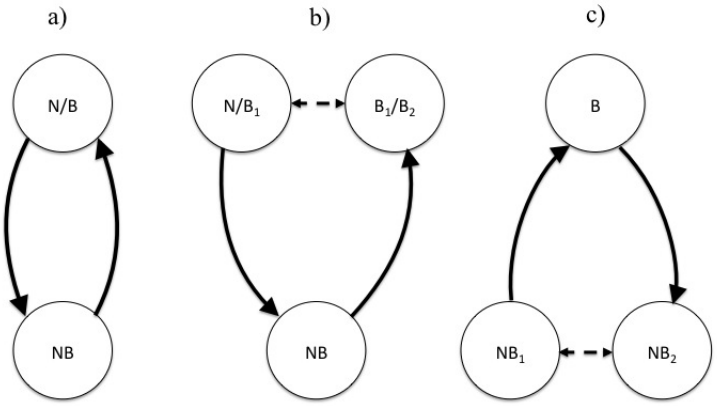


Figure 1: Conceptual models illustrating types of dispersal in migratory species. Solid lines indicate migratory movements and dotted lines represent dispersal. a) Philopatry/Site fidelity: In this case, an individual migrates from its natal (N) or breeding (B) site to its non-breeding (NB) site and then returns to these sites in subsequent years; b) Breeding-season dispersal: In this case, an individual migrates from its natal or breeding site to its non-breeding site but the following year settles in a new location to breed. If the individual is a juvenile selecting its first breeding location (B1), the dotted line represents natal dispersal. If the individual is an adult that moves to a new breeding location (B2), the dotted line represents breeding dispersal; c) Non-breeding dispersal: In this case, an individual migrates from one non-breeding site (NB1) to its breeding site but the following year selects a new non-breeding site (NB2). Following our definition, dispersal can also occur between other time periods used during some stage of the annual cycle, for example between stopover locations or molting sites.

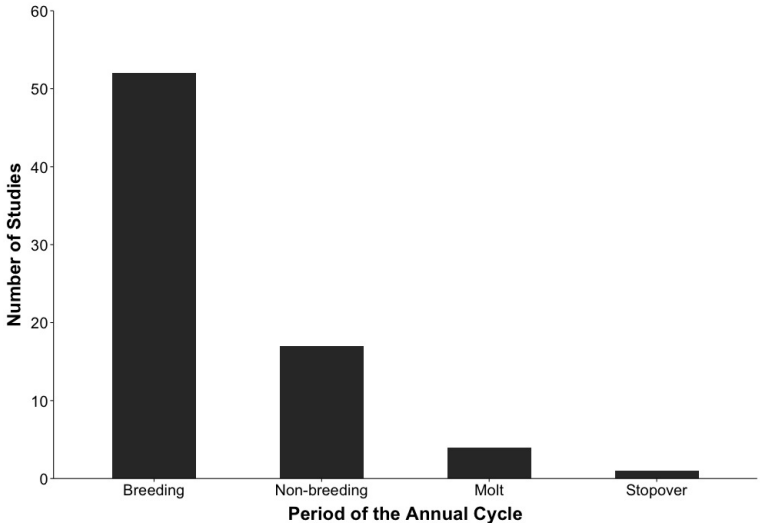


Figure 2: The number of studies focused on proximate causes of dispersal in migratory species during each period of the annual cycle. The breeding period is defined as the period during which the majority of reproductive activity takes place. The non-breeding is defined as the stationary period that does not serve as the primary reproductive period. We also included studies investigating the factors that influence dispersal between molting locations in birds and dispersal between stopover locations in all taxa.

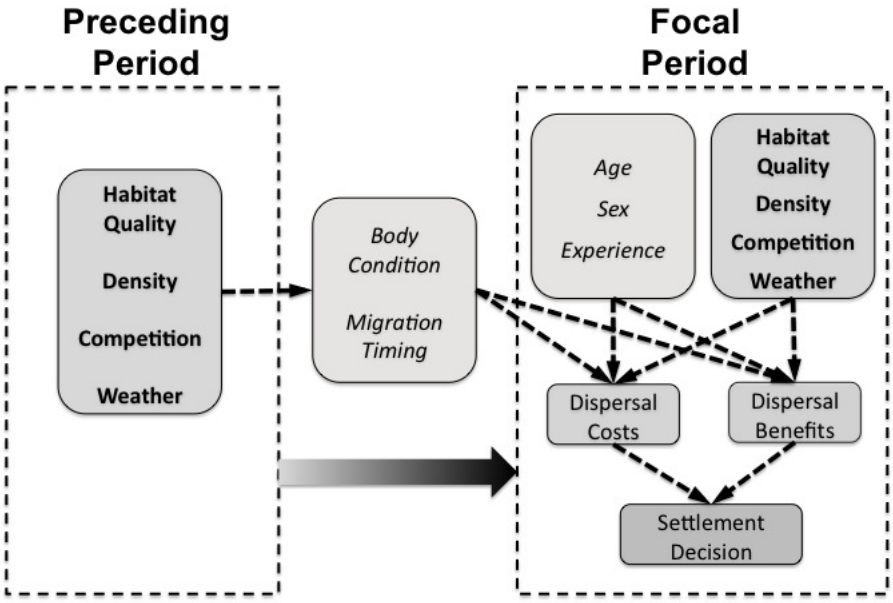


Figure 3: Conceptual diagram showing how carry-over effects influence costs/benefits of dispersal. The right panel illustrates the conventional approach to studying dispersal. In this case, researchers typically quantify how individuals-level traits (italics) or biotic and abiotic conditions (bold) influence the costs or benefits of dispersal. The balance of these costs and benefits, in turn, results in an individual settlement decision during the focal period. However, biotic and abiotic conditions experienced during the preceding period can influence the body condition and/or timing of individuals as they transition into the focal period. These carry-over effects can influence the costs or benefits of dispersal and therefore play an important role in settlement decisions.

3

ANNUAL VARIATION IN LONG-DISTANCE DISPERSAL OF A MIGRATORY BIRD DRIVEN BY BREEDING AND NON-BREEDING SEASON CLIMATIC CONDITIONS

ABSTRACT

Long-distance dispersal is a fundamental process in ecology and evolution but how factors experienced throughout the annual cycle influence these movements remains poorly understood. We used stable hydrogen isotopes to quantify the rate and direction of long-distance immigration into a population of American redstarts and to link these movements to breeding and non-breeding climate conditions and individual traits. Both natal and breeding dispersal were strongly influenced by the timing of breeding-season phenology, with both age classes more likely to disperse north in years with early phenology. Yearlings were also more likely to disperse north following winters with poor environmental conditions, demonstrating that carry-over effects from the non-breeding season influence natal dispersal in this species. Collectively, these results are consistent with the hypothesis that individuals use phenological cues to select breeding sites and indicate that the timing of migration relative to the phenology of breeding season resources influences long-distance dispersal in this species. Our results suggest that long-distance dispersal may allow individuals to rapidly respond to advancing phenology caused by global climate change, though their ability to do so may be constrained by long-term drying trends predicted for their tropical non-breeding grounds.

3.1 INTRODUCTION

Long-distance dispersal, defined as the movement of an individual beyond the normal boundaries of its population for the purpose of breeding, is one of the most important processes in ecology and evolution (Clobert et al., 2012). These movements can occur when yearlings move from their birth place to their first breeding location (i.e. natal dispersal) or when adults move between breeding locations in successive years (i.e. breeding dispersal). Although long-distance dispersal is generally rare in most species, many ecological and evolutionary processes are sensitive to the rate and magnitude of these movements, including local adaption and speciation (Green and Figuerola, 2005; Savolainen et al., 2007), population dynamics (Baguette, 2003; Bohrer et al., 2005), range expansion (Kot et al., 1996), and the response of species to climate change (Higgins and Richardson, 1999). Unfortunately, the inherent difficulty of tracking long-distance dispersal has limited progress on this subject and the factors that drive long-distance dispersal remain poorly understood in most species (Clobert et al., 2012).

Understanding the factors that influence long-distance dispersal is especially difficult in small migratory songbirds due to the scale of their annual movements and the challenges of tracking individual birds throughout their entire annual cycle (Winkler, 2005). Furthermore, there is growing evidence that many life history events, including dispersal, are shaped by the interaction of events across the annual cycle (Harrison et al., 2011). These seasonal interactions complicate the study of dispersal because decisions about where to breed may be determined partly by the conditions or events

experienced earlier in the year at locations separated by thousands of kilometers. Unfortunately, because most research on the causes of dispersal has focused exclusively on the role of events or conditions experienced on breeding grounds, the lack of information about how non-breeding season events influence long-distance dispersal represents a major impediment to developing a mechanistic understanding of long-distance dispersal in migratory species.

At present, only one study has provided direct evidence that seasonal interactions from the non-breeding season influence long-distance dispersal. Studds et al. (2008) found that American redstarts (*Setophaga ruticilla*) that occupied high-quality territories during their first winter departed earlier on spring migration and on average bred south of their natal latitude whereas individuals from low-quality non-breeding territories departed later and dispersed north of their natal latitude, demonstrating that habitat quality experienced during the non-breeding period is a primary driver of natal dispersal in this species.

Given the rapid environmental changes impacting migratory species during both their breeding and non-breeding periods (Faaborg et al., 2010), there is an urgent need for more research on how events experienced across the entire annual cycle interact to shape long-distance dispersal behavior. In this study, we used stable hydrogen isotopes to quantify the causes of long-distance immigration into a breeding population of American redstarts. The use of stable isotopes provided a spatially unbiased marker for estimating the origin of all individuals in our population, allowing us to address the following questions: 1) How do climate conditions experienced across the annual cycle influence the source of immigrants in a breeding popula-

tion? and 2) What individual-level traits influence long-distance dispersal decisions?

3.2 METHODS

American redstarts are long-distance migratory birds that breed throughout North America and winter in the Caribbean and Latin America (Sherry and Holmes, 1997). From 2009-2012, we studied a breeding population of redstarts at the Patuxent Research Refuge in Laurel, MD ($39^{o}04$'N, $76^{o}47$'W). Upon capture, individuals were classified as either yearlings (1 year old) or adults ($>$ 1 year old) following Pyle et al. (1997), fitted with an aluminum USFWS leg band and a unique combination of plastic color bands, weighed to the nearest 0.1g, measured for body size (bill length, bill width, bill depth, tarsus length, and unflattened wing chord) to the nearest 0.5mm, and released. In addition, one tail feather (R3) and the distal 0.3mm of each middle claw were sampled from each bird for stable hydrogen and stable carbon isotope analyses, respectively (see Appendix B for further details about field methods and isotope analysis).

We used the stable hydrogen isotope values from feather samples (δ^2H_f) to probabilistically determine the origin of all individuals breeding in our study population. This method relies on the latitudinal gradient of abundance of hydrogen isotopes in North American precipitation and the fact that this isotopic gradient is incorporated into bird feathers (Hobson et al., 2012). Because redstarts grow their feathers on their breeding or natal grounds prior to fall migration (Pyle et al., 1997), the stable hydrogen isotope abun-

dance in feathers of birds sampled during one breeding season reflects the geographic origin of these individuals from the previous year, providing a spatially unbiased estimate of long-distance dispersal (van Wilgenburg et al., 2012).

To determine the origin of all unknown-origin individuals in our population, we first estimated year-specific distributions of local δ^2H_f values using δ^2H_f values from individuals known to have bred at the study site the previous year. We then used these distributions to probabilistically determine the origin (northern, local, or southern) of all unbanded individuals based on a predefined odds ratio for correctly classifying individuals as local (van Wilgenburg et al., 2012). Thus, individuals with δ^2H_f values consistent with northern or southern origins are likely to be long-distance dispersers. Given the low resolution of stable isotopes (Langin et al., 2007), individuals categorized as "local" likely included both philopatric individuals (i.e. originating at our study site) and short-distance dispersers that recruited from the surrounding region, although it is difficult to translate δ^2H_f values directly into geographic distances. To test the sensitivity of our results to the threshold used to classify individuals as local, we carried out the assignments using three progressively stringent thresholds (4:1 odds, 9:1 odds and 19:1 odds) and performed all analyses under each scenario (see appendix B for further details). However, because results were qualitatively similar across odds ratios, only results from the 4:1 odds ratio are presented in the text. Results based on the 9:1 and 19:1 odds ratios are presented in Appendix C.

Statistical Analysis

We used proportional odds (PO) ordinal regression to determine how two climate variables and five individual-level factors influence long-distance dispersal (Guisan and Harrell, 2000). For our model, we considered origin as an ordinal factor with three levels defined by their spatial arrangement (south $<$ local $<$ north). The PO model assumes that the effects of predictor variables are equal across all categories of the response variable. To test that our data conformed to the PO assumption, we fit a global model for each odds ratio containing all predictor variables. We then relaxed the PO assumption for each predictor and used likelihood ratio tests to determine whether this nominal model improved the fit compared to the PO model. For our data, the nominal models did not fit significantly better than PO models, indicating the PO assumption was not violated for any predictor.

To determine which predictors influence long-distance dispersal, we used a hierarchical model selection approach (Bulluck and Buehler, 2008), which allowed us to focus on biologically-based hypotheses without testing all possible models (Burnham and Andersen, 2002). For this approach, we defined three suites of models and used Akaike's information criteria for small samples (AIC_c) to rank models within each suite. Any model with $\Delta AIC_c < 2$ was carried over to the next suite. The use of 2 as a threshold for model selection is recommended by Burnham and Andersen (2002) and is a conservative approach to model selection (Bulluck and Buehler, 2008). Suite I modeled dispersal status as a function of the main effects of age class

(yearling vs. adult), sex, and year, which have all been shown to influence dispersal in songbirds (Paradis et al., 1998).

Suite II included the top models from suite I plus the main effects of body condition, body size, non-breeding territory quality and the interaction of these variables with age class. Both body condition and body size have been linked to dispersal in several species of long-distance migratory birds and these effects are often stronger for natal than for breeding dispersal (Pärt, 1990; van der Jeugd, 2001). Body size was determined using principle component analysis (PCA) based on wing chord and tarsus length, with the first PCA score used as a measure of overall body size (Marra and Holmes, 2001). These scores were then regressed against body mass and the residuals were used as an estimate of body condition (Marra and Holmes, 2001). We used stable carbon isotopes from claw samples (δ^{13}C) to infer non-breeding territory quality. Stable-carbon isotope signatures of plants in the tropics vary by water availability (Michener and Lajtha, 2008), which is positively correlated with the abundance of soft bodied insects (Studds and Marra, 2007). Thus, the amount of δ^{13}C in tissues can be used as a proxy for habitat quality for insectivorous birds such as redstarts (Marra et al., 1998), with more negative values indicating wetter, higher quality habitat and more enriched values indicating drier, lower quality habitat. Turnover of δ^{13}C in claws is on the order of weeks (Hahn et al., 2014), allowing us to use claw samples collected upon arrival on the breeding grounds to infer territory quality experienced during the preceding winter (Reudink et al., 2009a).

Suite III included the top models from suite II plus the main effects of breeding-ground phenology and large-scale habitat quality in the Caribbean and the interaction of these variables with age class. We predicted that

individuals from southern latitudes would disperse north in years when phenology occurs comparatively early whereas individuals from northern latitudes will disperse south in years when phenology occurs later. We used the peak blossom date of cherry trees (*Prunus* × *yedoensis*) on the National Mall in Washington, D.C. (~30km from our study site) as a surrogate for the phenology of plants and insects in the region surrounding our study site. The peak cherry blossom date is tracked annually by the US National Park Service (`www.nps.gov/cherry/cherry-blossom-bloom.htm`), providing a standard measure for comparing annual variation in the timing of phenology for our study site.

To quantify large-scale habitat quality experienced by redstarts during the non-breeding season, we used the mean Normalized Difference Vegetation Index (NDVI) from January to March from Cuba (`http://pekko.geog.umd.edu/usda/test/`). NDVI values provide an estimate of net primary productivity, which is highly correlated with food abundance and habitat quality for American redstarts during the non-breeding period (Studds and Marra, 2007). Most redstarts breeding in the eastern United States winter in the Caribbean (Norris et al., 2006) and because NDVI values are correlated across the Greater Antilles (Wilson et al., 2011), values from Cuba should reflect conditions experienced by most redstart breeding at our study site. We chose to use NDVI values from January through March because this period has the largest impact on individuals transitioning into the breeding season (Studds and Marra, 2007; Wilson et al., 2011). Based on the observations of (Studds et al., 2008), we predicted that yearlings, but not adults, would be more likely to disperse north following winters with below-average primary productivity (low NDVI values) and more likely to disperse south

following winters with above-average primary productivity (high NDVI values). Both the peak cherry blossom date and late-season NDVI in Cuba showed substantial variation over the course of our study (Figure 4), providing a unique opportunity to test how these factors influence long-distance dispersal in redstarts.

All continuous variables were mean-centered prior to analysis to reduce co-linearity and missing values for individual-level factors were assigned a value of 0. Although including these mean values could lower our ability to detect individual-level effects, missing values accounted for only a small percentage ($< 2\%$) of our data and therefore likely had little effect on our conclusions. We considered any model from Suite III with $\Delta\text{AIC}_\text{c} < 4$ to be consistent with our data (Burnham and Andersen, 2002) but because our candidate models contained a mix of interaction terms, we were unable to use model-averaging to account for this model selection uncertainty. We considered coefficients with 95% confidence intervals that did not overlap zero to be significant predictors of dispersal status and interpreted consistency in the significance, sign, and magnitude of predictors across the candidate set and odds ratios as strong evidence that a factor influences long-distance dispersal. All models were fit in R v3.0.2 (R Core Team, 2013) using the clm function in the package ordinal v2013.9-30 (Christensen, 2013).

3.3 RESULTS

Immigration Patterns

Over the course of our study, we sampled 320 redstarts and our data indicate that long-distance dispersal is relatively rare in this species, with the majority of individuals (85.6%) in both age and sex classes having $\delta^2 H_f$ values consistent with a local origin (Table C1). In addition, our data indicated that while the majority of immigrants in our population originated to the north of our study site, the source of immigrants showed significant annual variation over the course of the study (Figures 4; C1). From 2009-2011, the majority of immigrants into our population (78.4%) originated from north of our study site (Figure 4; Table C1). In 2012, however, the majority of immigrants (70%) originated from south of our study site (Figure 4; Table C1).

The role of climate

Overall, the most consistent factor influencing dispersal status in our models was breeding-season phenology, with every candidate model in the 4:1 set containing either the additive or multiplicative effects of the peak cherry blossom date (Table 1). As predicted, the coefficients were negative in all models, indicating that the odds of originating from the south increase in years with early phenology (Figure 5). Models with the additive effect of phenology accounted for 0.73 of the cumulative weight of the candidate set

and coefficients were significant in all models. Coefficients for the multiplicative effects of phenology were also negative for both age classes (unweighted average: yearlings: $\hat{\beta}$ = -.284 ± 0.081; adults: $\hat{\beta}$ = -0.165 ± 0.007) and 95% confidence intervals did not overlap zero in 14 of the 15 models (Table 1). The magnitude and significance of the coefficients were largely consistent across odds ratios (Table C2; Figure C2), providing evidence that both long-distance natal and breeding dispersal were sensitive to the influence of breeding-season phenology.

NDVI was included in 14 of the 15 (93.3%) top models in the 4:1 set (Table 1), indicating that large-scale habitat quality during the non-breeding season also had an influence on subsequent long-distance dispersal, though there was some uncertainty regarding the interaction between non-breeding conditions and age. Of the 4:1 candidate models, the top model contained the interaction of NDVI with age and multiplicative models accounted for 0.71 of the cumulative weight (Table 1). Furthermore, the coefficients for the effect of NDVI on natal dispersal were negative and significant ($\hat{\beta}$ = -4.146 ± 1.28) in all multiplicative models in the 4:1 candidate set, indicating that yearlings, but not adults, were more likely to originate from the south following winters with below-average productivity (Figure 6). In contrast, models with the additive effect of NDVI were favored in the 9:1 candidate set (0.79 of the cumulative weight) and 19:1 candidate set (.97 of the cumulative weight; Table C2). Coefficients for additive effects of NDVI were negative and significant ($\hat{\beta}$ = -2.47 ± 0.178) in all 9:1 models, suggesting a significant influence of NDVI on long-distance dispersal. However, for models containing multiplicative effects of NDVI, the magnitude of the effect of NDVI on natal dispersal ($\hat{\beta}$ = -2.398 ± 1.54) was larger than the effect of

NDVI on breeding dispersal ($\hat{\beta}$ = -1.436 ± 2.14; Figure C3), though these coefficients were not significant. Only one model in the 19:1 set contained the interaction of NDVI with age, and coefficients were similar in magnitude to the 9:1 models (yearlings: β = -2.32 ± 2.6 adults: β = -1.48 ± 1.9). The wide confidence intervals for natal dispersal coefficients under the 9:1 or 19:1 odds ratios suggest that we did not have the statistical power to detect significance under these restrictive thresholds. However, the significant results under the 4:1 threshold and the consistency of the coefficients across the three candidate sets suggest that non-breeding conditions have a stronger impact on long-distance natal dispersal than on breeding dispersal.

The role of individual-level traits

Of the individual-level traits that we included in our models, only age class was consistently included in the top models (Table 1; Table C2). Over the four years of our study, the immigration rate was higher for yearlings (18.1%) than for adults (11.2%; Table C1), indicating that long-distance natal dispersal is more common than long-distance breeding dispersal in this species. However, the immigration rates for each age class showed substantial variation among years and in both 2011 and 2012, our population received more adult immigrants than yearlings (Figure 4; Table C1).

Across all years, immigration rates were generally lower for females (11.02%) than for males (14.68%) but sex was not included in any of the top models (Table 1; Table C2). Both body condition and non-breeding territory quality (δ^{13}C) were selected in 5 of the 15 models in the 4:1 set but the confidence

intervals for all coefficients overlapped zero in all models (Table 1; Table C2). Body size was not included in any of the top models (Table 1; Table C2). Overall, these results suggest that the annual variation in immigration into our population were not driven by the individual-level traits included in our analysis.

3.4 DISCUSSION

In this study, we used a spatially-unbiased intrinsic marker to uncover large-scale annual variation in the source of immigrants into our study population. Overall, and particularly from 2009-2011, the majority of immigrants into our population had δ^2H_f values consistent with northern origins. Redstart breeding densities increase to the north of our study site and decrease to the south (Norris et al., 2006), and this northern-bias might be expected if the northern portion of the breeding range produces more potential dispersers than the southern portion (Graves, 1997). However, in 2012 we observed the opposite pattern, with virtually all immigrants originating from south, suggesting that breeding density is not the sole driver of immigration into our population. The sharp distinction between years and the consistency across age and sex classes suggest that these patterns are not due to aberrant δ^2H_f values, such as local individuals with abnormally enriched or depleted δ^2H_f values (Langin et al., 2007) or to individuals molting their feathers at southern latitudes during migration (Reudink et al., 2008).

Instead, our data provide evidence that in certain years, large-scale environmental conditions resulted in a significant influx of southern immigrants

and a corresponding decrease in northern immigrants. In 2009, our population received an influx of yearling immigrants from the south (Figure 4). The preceding winter, habitat quality was far below average across the Caribbean (Figure 4), conditions which are known to delay departure on spring migration for redstarts (Marra et al., 1998). If individuals use phenological cues to select breeding sites (Studds et al., 2008; Husek et al., 2014), individuals that would normally breed in the southern portion of the breeding range were likely forced to migrate further north to locate suitable breeding sites Studds et al. (2008). In contrast, immigration of southern yearlings was low or absent in 2010 and 2011, years with above average non-breeding conditions (Figure 4). These results corroborate the earlier findings of Studds et al. (2008) and provide evidence that carry-over effects from the non-breeding season are a primary driver of natal dispersal in this species.

In addition to the influence of non-breeding conditions, our results indicate that the timing of breeding season phenology has a strong influence on both natal and breeding dispersal in American redstarts. In 2012, the peak cherry blossom date occurred approximately two weeks earlier than normal, resulting in a striking influx of southern immigrants into our population and virtually no northern immigrants (Figures 4; C1). Under these conditions, individuals from southern latitudes likely arrived at their natal or previous breeding location after food resources had peaked and, similar to the consequences of delayed departure from the non-breeding grounds, were forced to continue migrating to locate breeding sites with optimal resource levels. Although the sensitivity of adults to phenological cues is surprising, other studies of migratory birds have also found that breeding dispersal is influ-

enced by climate conditions (Møller et al., 2006; Figuerola, 2007). Thus, although long-distance breeding dispersal is generally rare in most birds (Paradis et al., 1998), these results indicate that experienced breeders may be more sensitive to extreme climate conditions than is commonly believed. If true, breeding dispersal may play an underappreciated role in shaping population dynamics, gene flow, and responses to climate change in many species.

Direct evidence linking climate conditions to long-distance dispersal behavior is rare (Møller et al., 2006; Massot et al., 2008; Husek et al., 2014) and our results have important implications for predicting how migratory birds will respond to climate change. As breeding-season phenology in temperate areas has advanced in recent decades, there is evidence that some migratory species have not advanced their arrival dates on the breeding grounds to keep pace (Both and Visser, 2001). As a result, in years with early breeding-season phenology, the resources necessary for reproduction peak before individuals initiate reproductive activities (Both et al., 2006) and this phenological mismatch has been linked to reduced reproductive success in several long-distance migratory bird species (Both et al., 2006; Saino et al., 2011). As temperate areas continue to warm, there is concern that the magnitude of phenological mismatches will increase, possibly resulting in declines and extinction of many migratory bird species (Møller et al., 2008).

At present, most research on the response of migratory birds to climate change has focused on the ability of individuals to adjust the speed of migration in response to environmental conditions experienced *en route* (Marra et al., 2005; Hurlbert and Lian, 2012) or on the evolutionary potential of

populations to adjust the timing of migration or breeding over longer time scales (Charmantier and Gienapp, 2013). In contrast, research on the ability of individuals to respond to advancing phenology via long-distance dispersal has largely been neglected. Nonetheless, evidence that migratory birds use phenological cues to select breeding sites is beginning to emerge. For example, Husek et al. (2014) recently demonstrated that pied flycatchers (*Ficedula hypoleuca*) were more likely to disperse north in years with warm spring temperatures and early food resource phenology but more likely to return to their natal area in years with average temperatures and food resource phenology. Though the dispersal events recorded by Husek et al. (2014) were restricted to a 10-km latitudinal gradient, our results and those of (Studds et al., 2008) indicate that similar behaviors occur in American redstarts over regional spatial scales. Although additional work is needed to determine if these behaviors are widespread in other species, these results could explain why phenological mismatches have not been observed in many species (Jones and Cresswell, 2010) and why individual-level phenological mismatches often have little impact on population trends (Dunn and Møller, 2013).

Even if long-distance dispersal buffers individuals against the impacts of temperate warming, our results indicate that the ability of individuals to respond to breeding-season phenology may be constrained by conditions experienced during the previous non-breeding season. Climate models predict that the Caribbean basin will receive significantly less precipitation in the coming century (Neelin et al., 2006), which will result in overall poorer habitat quality for American redstarts and many other insectivorous songbirds that winter in the Caribbean. Drier conditions will result in lower food

resources, delaying departure on spring migration, and forcing individuals to disperse farther north to synchronize reproductive efforts with optimal breeding conditions. Unfortunately, advancing breeding-season phenology on temperate breeding grounds may confound these effects. At present, most assessments of climate change vulnerability focus on the impacts of temperate climate change, but our results underscore the importance of considering how individual organisms respond to shifting environmental conditions experienced throughout their entire annual cycle (Small-Lorenz et al., 2013).

Finally, our results demonstrate the potential of intrinsic markers such as stable isotopes to reveal novel insights into the factors influencing long-distance dispersal. Although the spatial resolution of stable isotope data is low, the ability to collect large amounts of spatially unbiased dispersal data can uncover patterns that would be impossible to detect using conventional mark-recapture methods. As researchers continue to seek a mechanistic understanding of long-distance dispersal (Travis et al., 2012), further development of these methods, combined with a "full life-cycle" perspective that considers how events across the annual cycle influence dispersal, will be critical to understanding and predicting the impacts of climate change on the planet's biodiversity.

Model	k	AIC_c	ΔAIC_c	w_i
Age + **Phenology** + NDVI + **Age × NDVI**	6	320.15	0.00	0.18
Age + **Phenology** + NDVI + **Age × Phenology** + **Age × NDVI**	7	320.26	0.11	0.17
Age + **Phenology** + **NDVI**	5	321.65	1.50	0.08
Age + **Phenology** + NDVI + Condition + **Age × NDVI**	7	321.80	1.65	0.08
Age + **Phenology** + NDVI + δ13C + **Age × NDVI**	7	321.86	1.71	0.08
A*ge* + **Phenology** + NDVI + Condition + **Age × Phenology** + **Age × NDVI**	8	321.97	1.82	0.07
Age + **Phenology** + NDVI + δ13C + **Age × Phenology** + **Age × NDVI**	8	322.10	1.95	0.07
Age + **Phenology**	4	322.74	2.59	0.05
Age + **Phenology** + *NDVI* + **Age × Phenology**	6	323.22	3.07	0.04
Age + **Phenology** + *NDVI* + Condition	6	323.28	3.13	0.04
Phenology + **NDVI**	4	323.34	3.19	0.04
Age + **Phenology** + *NDVI* + δ13C	6	323.40	3.25	0.03
Age + **Phenology** + NDVI + Condition + δ13C + **Age × NDVI**	8	323.57	3.42	0.03
Age + *Phenology* + NDVI + Condition + δ13C + *Age × Phenology* + **Age × NDVI**	9	323.86	3.71	0.03
Age + **Phenology** + **Age × Phenology**	5	323.93	3.78	0.03

Table 1: Summary of model selection results for dispersal assignments based on 4:1 odds ratio. Only models with $\Delta AIC_c < 4$ in the final model suite are shown. Coefficients for which the 95% confidence intervals (CI) did not contain zero are shown in bold. Coefficients for which the 90% CI did not contain zero are shown in italics.

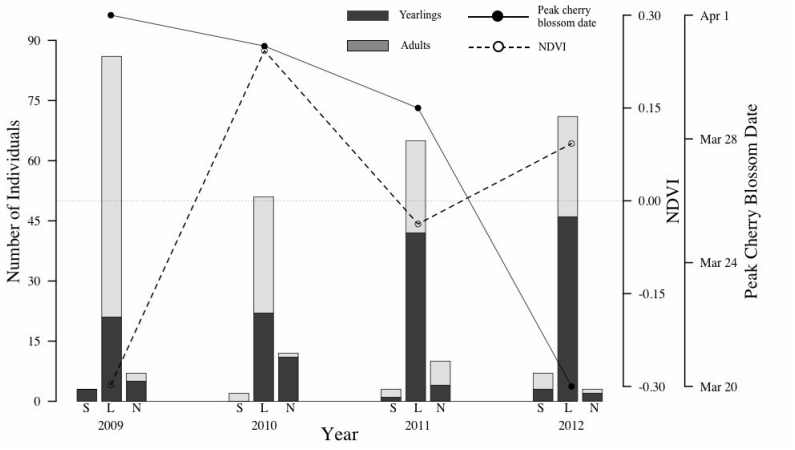


Figure 4: Patterns of immigration into the study population and variation in climate variables from 2009 to 2012. Bars show the number of individuals within each age class assigned to each dispersal category based on a 4:1 odds ratio. Within each year, the left bar shows the number of individuals with a southern origin ("S"), the center bar shows the number of local individuals ("L"), and the right bar shows the number of individuals with a northern origin ("N"). The solid line and closed circles show the peak cherry blossom date for each year while the dashed line and open circles show the mean NDVI value from January to March in Cuba. NDVI values are mean-centered so positive values (above the dotted line) represent above average primary productivity and negative values (below the dotted line) represent below average primary productivity.

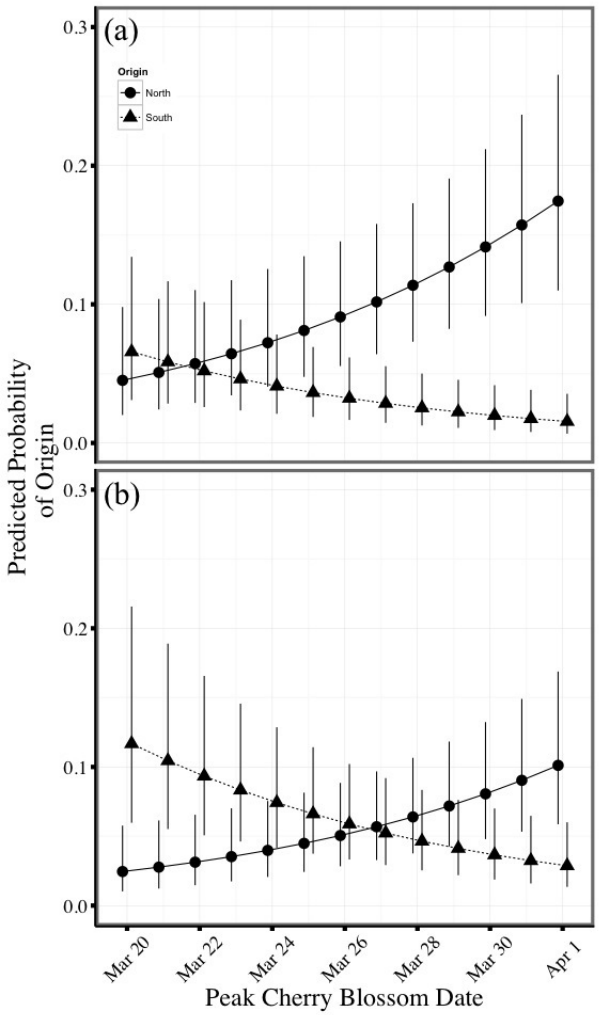


Figure 5: Predicted probability of origin as a function of cherry blossom phenology on the breeding grounds based on the top model from the 4:1 odds ratio candidate set for (a) yearlings and (b) adults. Horizontal bars show 95% CI.

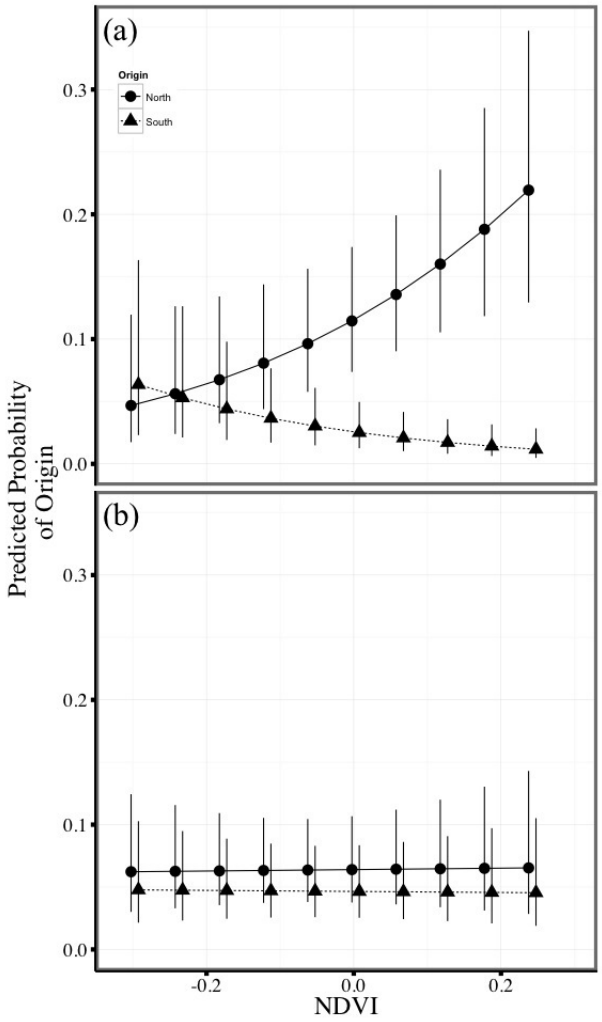


Figure 6: Predicted probability of origin as a function of the Normalized Difference Vegetation Index (NDVI) values from January to March in Cuba based on the top model from the 4:1 odds ratio candidate set for (a) yearlings and (b) adults. NDVI values were mean-centered on the long-term average, thus positive values indicate higher quality conditions and negative values indicate lower quality conditions. Horizontal bars show 95% CI.

4

HABITAT FEATURES AND LONG-DISTANCE DISPERSAL MODIFY THE USE OF SOCIAL INFORMATION BY A MIGRATORY BIRD

ABSTRACT

The processes by which individuals select breeding sites have important consequences for individual fitness as well as population- and community-dynamics. Although there is increasing evidence that many animal species use information acquired from conspecifics to assess the suitability of potential breeding sites, little is known about how the use of this social information is modified by biotic and abiotic conditions. We used an automated playback experiment to simulate two types of social information, post-breeding public information and pre-breeding location cues, to determine the relative importance of these cues for breeding site selection by a migratory songbird, the American redstart (*Setophaga ruticilla*). In addition, we used stable hydrogen isotopes to determine the dispersal status of individuals that responded to our experimental treatments and quantify whether long-distance dispersers use different social cues to select breeding sites compared to philopatric individuals. We found that points that received pre-breeding location cue treatments were significantly more likely to be settled by redstarts than control points that received no playback. However, we found no evidence the redstarts used post-breeding public information gathered during one season to select breeding sites the following year. Breeding site habitat structure was also a strong predictor of

settlement probability, indicating that redstarts modified the use of social information based on habitat cues. Furthermore, stable hydrogen isotope signatures from individuals that responded to location cue treatments suggest that long-distance dispersers may rely more heavily on these cues than local recruits. Collectively, these results indicate that redstarts use multiple sources of information to select breeding sites, which could buffer individuals from selecting suboptimal sites when they breed in unfamiliar locations or when habitat quality becomes decoupled from social cues.

4.1 INTRODUCTION

The ability to locate and select high-quality breeding sites is a key behavioral process that links individual fitness to population- and community-level dynamics, including population regulation (Fretwell and Lucas, 1970; Pulliam, 1988), community assembly (Fletcher, 2008; Betts et al., 2010), and maintaining biological diversity (Ward and Schlossberg, 2004). Understanding the cues that individuals use to assess and select breeding sites is thus a central question in ecology, evolution, and conservation (Morris, 2003; Danchin et al., 2004; Ahlering and Faaborg, 2006). In recent decades, empirical research has demonstrated that information acquired from conspecifics, termed *social information*, is widely used by many species to assess the quality of potential breeding sites (Reed et al., 1999; Valone, 2007). Compared to other sources of information (e.g. habitat features or previous reproductive success), social information is assumed to be relatively efficient to collect, can provide information about habitat quality even when the features that

influence fitness are not apparent, and is available to most individuals regardless of age or reproductive experience (Szymkowiak, 2013). However, not all types of social information are equally reliable and understanding when and under what conditions individuals use different types of social information remains poorly understood (Doligez et al., 2003; Danchin et al., 2004; Stamps and Krishnan, 2005).

Social information is generally divided into two categories: information about the presence/absence of conspecifics, termed *location cues*, and information about the reproductive performance of conspecifics, termed *public information* (Danchin et al., 2004). When the quality of breeding sites is predictable across years, both cues can provide information about the location of suitable breeding sites. However, while the presence of breeding individuals is generally associated with suitable habitat, location cues do not provide direct information about the relative quality of different sites and under certain circumstances it is possible for location cues to become uncoupled from habitat quality (Schlaepfer et al., 2002). In contrast, because public information is based directly on conspecific performance, it is generally a highly reliable cue for assessing breeding site quality. For this reason, public information should be favored over location cues in stable environments (Doligez et al., 2003). Despite this prediction, empirical studies have demonstrated that location cues are widely used by many species (e.g., Ahlering et al., 2006; Serrano et al., 2004; Szostek et al., 2014). Explaining the coexistence of these two strategies is an important step to developing a general theory of breeding site selection (Szymkowiak, 2013).

Several hypotheses may explain why individuals use location cues even when public information provides more reliable information about breeding

site quality. First, when all individuals in a population breed synchronously, young individuals do not have the opportunity to gather public information (Nocera et al., 2006) and may be forced to rely on location cues (Doligez et al., 2004). Second, dispersers forfeit any previously acquired public information when they move to new locations and therefore immigrants may be more reliant on location cues than philopatric individuals (Szostek et al., 2014). Although inter-specific comparisons provide some empirical support for both hypotheses (Reed et al., 1999; Stamps and Krishnan, 2005), the dynamics of populations are ultimately influenced by intra-specific variation in habitat selection behavior (Kristan, 2003). Therefore, linking individual behavior to population dynamics requires understanding the causes of intra-specific variation in breeding site selection. Few studies, however, have simultaneously quantified the relative importance of public information and location cues for individuals within the same population (but see Doligez et al., 2004; Nocera et al., 2006).

In this study, we simulated post-breeding public information and pre-breeding location cues to experimentally test the relative importance of each cue for breeding site selection in a migratory songbird, the American redstart (*Setophaga ruticilla*). We tested the following predictions:

1) *Redstarts use both pre-breeding location cues and post-breeding public information to select breeding sites:* Several studies have documented the use of pre-breeding location cues by adult American redstarts (Hahn and Silverman, 2006; Fletcher, 2007) and therefore we predicted that this would an important source of social information for birds in our population. The use of post-breeding public information by redstarts has not been studied

but Betts et al. (2008) experimentally demonstrated that individuals of the closely related black-throated blue warbler (*Setophaga caerulescens*) monitor the reproductive performance of conspecifics and use this information to select breeding sites the following year. Given the close phylogenetic relationship between these two species (Lovette et al., 2010) and the similarity of their breeding habitat, we predicted that redstarts would also use post-breeding public information to select breeding sites.

2) *Pre-breeding location cues are a more important source of information than post-breeding public information:* Black-throated blue warblers often produce two broods per season and this asynchrony provides individuals from early broods the opportunity to gather public information from the territories of successful second broods (Betts et al., 2008). In contrast, because redstarts are obligate single brooders (Sherry and Holmes, 1997), their short, synchronous breeding season may prevent newly fledged redstarts from gathering public information (Nocera et al., 2006). Therefore, we predicted that post-breeding public information would be a less important source of social information than pre-breeding location cues for redstarts.

3) *The use of social information differs between adults and yearlings due to asynchronous opportunities to collect public information:* Although newly fledged redstarts may not have the opportunity to collect public information, many yearling males in our population remain unmated throughout the breeding season (Section 5.3) and these individuals provide a potential pool of prospectors that could gather and use post-breeding public information (Doligez et al., 2004). Therefore, we predicted that post-breeding public

information would be a more important cue for adults whereas pre-breeding location cues would be more important for first-time breeders.

4) *Long-distance dispersal modifies the use of social information cues:* Because dispersing individuals cannot rely on post-breeding public information gathered the previous year, we predicted that immigrants would be more likely to use pre-breeding location cues than philopatric individuals.

4.2 METHODS

Study species and study site

American redstarts are long-distance Neotropical migratory songbirds that breed throughout North America and winter in the Caribbean and Latin America (Sherry and Holmes, 1997). Since 2009, we have studied a large population of redstarts breeding at the Patuxent Research Refuge in Laurel, MD ($39^{o}04$'N, $76^{o}47$'W). The 250ha study area consists primarily of beech-dominated bottomland forests adjacent to the Patuxent River. Dominant tree species at the site include American beech (*Fagus grandifolia*), American elm (*Ulmus americana*), Tuliptree (*Liriodendron tuipifera*), sweetgum (*Liquidambar styraciflua*) and several species of oak (*Quercus* sp.). Understory species include American hornbeam (*Carpinus caroliniana*), Pawpaw (*Asimina triloba*) and several species of maple (*Acer* sp.).

Male redstarts generally begin to arrive at our study site in mid-April (range: 17 April - 21 April), followed by females approximately 7-10 days later. Nesting commences shortly after the arrival of females and all nests

in our population fledge between 31 May and 2 July. Parents remain with fledglings on breeding territories for 1-3 weeks, at which point fledglings become independent. Redstarts are obligate single brooders (Sherry and Holmes, 1997) and after a successful nesting attempt, pairs do not attempt to rebreed. Therefore, all territories at our study site are abandoned by late-July.

Experimental Design

To test our predictions, we simulated both post-breeding public information and pre-breeding location cues at points located within the larger population of redstarts at our study site. The basic experimental design consisted of simulating post-breeding public information cues during the fledging period of one breeding season (to simulate successful territories) and then simulating pre-breeding location cues at a different set of locations during the arrival period the following year (to simulate the presence of territorial males). During the second year of the experiment, all points were monitored to determine the number of redstarts holding territories in the vicinity of each point. We repeated this design twice, with the first round initiated during the 2011 fledging period and completed during the 2012 arrival period (hereafter referred to as the 2012 round) and the second initiated in 2012 and completed in 2013 (hereafter referred to as the 2013 round).

In 2011 and then again in 2012, we selected points for our experiment and randomly assigned each point to one of three treatments: post-breeding public information (n = 20), pre-breeding location cues (n = 20), or control (n

= 30). To minimize the influence of habitat structure or previous experience, we selected points that were similar in general habitat structure (e.g. forested) and that were $\geq$ 150m from existing redstart territories. Additionally, all points were separated by >250m to ensure independence among the experimental treatments.

For both the post-breeding public information and pre-breeding location cue treatments, playback was broadcast using a CD player housed in a waterproof box and connected to two speakers mounted 2m above the ground, 20m apart, and facing in opposite directions. An automated timer turned on the playback each morning at 0500 and broadcast the treatment until 1400. Each song track was separated by 15 seconds of silence and was alternated between the two speakers every 5 minutes to minimize habituation. Post-breeding public information treatments were broadcast from June 1st to August 1st and consisted of locally recorded male and female redstarts vocalizing while feeding young and fledgling begging calls. Pre-breeding location cue treatments were broadcast from April 10th to May 15th and consisted of locally recorded territorial male songs. In 2013, one pre-breeding location cue station failed and was removed from analysis, resulting in a total of 19 replications for this treatment. Because both anthropogenic and heterospecific cues can influence settlement patterns of birds, we chose not to apply any playback at control points (Betts et al., 2008).

To determine whether redstarts collect post-breeding public information by observing the reproductive performance of conspecifics (i.e. prospecting), we conducted 10 minute point counts once per week during the public information treatment period at all post-breeding public information and control points. All point counts were conducted between 0600 and 1000 on

days without rain or wind. After a 2 minute settling period, any redstart seen or heard within 50 meters of point during the 10 minute point count was considered a prospector and we used a logistic regression to compare the number of prospectors at public information and control point. During the post-breeding period, the age and sex of redstarts with female-like plumage cannot be reliably determined (Pyle et al., 1997) so we did not record the age or sex of prospectors unless they were adult males.

During the 2012 and 2013 arrival periods, all treatment and control points were surveyed daily to record the presence of male redstarts. Any male that was observed within 75 meters of a point on $>$ 3 consecutive days and responded aggressively to conspecific song was considered to be settled at that point.

Measuring habitat structure

Although treatment and control points were visually inspected to ensure similar habitat structure, fine-scale differences in habitat features could still have influenced settlement decisions. To control for the influence of habitat structure, we quantified vegetation features within a 5-m radius circle centered on each point and within three more circles located 25-m from the center at 0°, 120°, and 240° (Tarof et al., 2004). Within each circle, we measured five habitat features: the number of saplings ($<$ 3cm diameter at breast height (DBH)), the number of trees ($>$ 3 cm DBH), the number of beech trees, the percent shrub cover, and the percent canopy cover. For each tree, DBH was measured 2m above the ground using a diameter tape.

We chose to record the number of beech trees because this is the preferred nesting tree for redstarts at our study site (C. Rushing *unpubl. data*) and therefore may influence settlement decisions. Shrub cover was visually estimated as the percent of the ground covered in shrubs and was recorded on a scale of 1-4 (1 = 0-25%; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%). To estimate percent canopy cover, we photographed the canopy directly above each circle using a Nikon Coolpix 990 digital camera fitted with a Nikon LC-ER1 8mm 180° fisheye converter and vertically mounted on a tripod. We then used Gap Light Analyzer 2.0 (Frazer et al., 1999) to quantify the percent canopy cover within each photograph. In addition to these five habitat features, we also estimated the mean tree basal area and the total basal area (TBA) within each circle. We calculated tree basal area as $0.005454xDBH^2$ (James and Shugart Jr, 1970). To estimate TBA, we converted the tree basal areas to basal area/acre ($0.00007854x$tree basal area), and then summed these measures for all trees within the circle (James and Shugart Jr, 1970).

For each habitat feature, measurements were averaged across the four circles to derive a single estimate for the entire point. A multi-variate ANOVA indicated that the three treatment levels did not systematically differ in any of the measured habitat features ($F_{14,132} = 1.22, p = 0.27$). Therefore, we then used a principle component analysis (PCA) to reduce the number of dimensions for the habitat structure. The first three principle components described over 75% of the variation in habitat structure (Table D1) and we included these scores in our analysis of settlement at playback points (see below).

Inferring dispersal status

To test our prediction about the influence of long-distance dispersal on the use of social information, we attempted to capture all males that responded to our experimental treatments and used stable hydrogen isotopes to determine the dispersal status of each individual. All individuals were captured in mist nets using decoys and playback of conspecific song. After capture, each individual was classified as either a yearling (1 year old) or an adult (> 1 year old) following Pyle et al. (1997), fitted with an aluminum USFWS leg band and a unique combination of plastic color bands, weighed to the nearest 0.1g, measured for body size (bill length, bill width, bill depth, tarsus length, and unflattened wing chord) to the nearest 0.5mm, and released.

During banding, we also collected one tail feather (R3) for stable hydrogen isotope analysis. Stable hydrogen isotopes in feather samples ($\delta^2 H_f$) vary as a function of latitude in North America (Hobson et al., 2012) and can be used to infer long-distance dispersal in migratory birds (van Wilgenburg et al., 2012). Because redstarts grow tail feathers at their breeding location prior to fall migration, $\delta^2 H_f$ values from redstarts that bred at our study site in 2011 and 2012 and were recaptured in 2012 and 2013 provided the expected $\delta^2 H_f$ distributions for birds originating at our study site during the years of our experiment. We then used these distributions to probabilistically determine dispersal status of individuals captured at playback stations following the methods described in Appendix B.

In addition to the individuals that responded to our experimental treatments, we also collected isotope data from 97 male redstarts (2012: n = 62,

2013: n= 35) in the general population at our study site. These data served as a baseline for comparing immigration patterns in our treatment groups.

Analysis

Do social information and habitat structure influence settlement decisions?

To determine whether playback treatments and habitat characteristics influenced settlement decisions of redstarts, we tested whether the probability that sites were settled by redstarts differed between treatments using a simple Bayesian model, which we refer to as the *settlement* model. We modeled whether or not each site was occupied by ≥ 1 redstart (denoted C_i) as a Bernoulli trial as follows:

$$C_i \sim Bernoulli\,(\psi_i) \tag{1}$$

$$logit\,(\psi_i) = \alpha + \beta_1 LC_i + \beta_2 PI_i + \beta_3 Year_i + \beta_4 PC1_i + \beta_5 PC2_i + \beta_6 PC3_i \tag{2}$$

where ψ_i is the probability of settlement at site i, LC_i and PI_i are dummy variables indicating whether site i received location cue treatment or post-breeding public information treatment, $Year_i$ is a dummy variable indicating whether the treatment was applied in the second year of the experiment, and $PC1_i$, $PC2_i$, and $PC3_i$ are the first three habitat scores for site i. In addition to the parameters listed in equation 2, we also derived posterior distributions for the difference in probability of settlement between each treatment and used the 95% credible intervals of these posteriors to deter-

mine whether the probability of settlement was higher at playback sites than controls and whether the probability of settlement differed between the two playback treatments. To determine whether the probability of settlement differed between age classes, we also fit the same model for yearlings and adults separately.

Does long-distance dispersal modify the use of social information?

To determine whether individuals that settled at playback sites were more or less likely to be immigrants than individuals from the general population, we modeled the total number of immigrants that settled in response to each treatment (denoted I_i) as a binomial variable as follows:

$$I_i \sim Binomial\,(N_i, p_i)$$

where N_i is the total number of individuals that settled at points with treatment level i and p_i is the probability that an individual from treatment i is an immigrant. A similar model was used to estimate the probability that an individual from the general population was an immigrant (p_{pop}) and the posterior distribution for the difference between p_i and p_{pop} (denoted p_{diff}) was used to determine whether immigration rates differed between treatment groups and the general population.

Estimation and model fit

Posterior distributions for each parameter were estimated using Markov chain Monte Carlo (MCMC) methods implemented in JAGS 3.4.0 (Plum-

mer, 2003) using the R2jags package (Su and Yajima, 2014) in R v3.0.2 (R Core Team, 2013). We chose uninformative priors for all parameters. Specifically, we used $Normal(0, 100)$ as a prior for regression parameters in the *settlement* model and $Uniform(0, 1)$ as a prior for both p_{i} and p_{pop} in the immigration model. Three chains were computed for each parameter and we stored 15 000 samples from each chain after discarding the first 10 000 iterations as burn-in. Convergence of the chains was assured by visual inspection of trace plots and by Gelman diagnostics (Brooks and Gelman, 1998).

To assess model fit, we used posterior predictive checking (Kruschke, 2011). For each model, we used draws from the posterior distribution of each parameter to simulate a data set of the same size as the observed data. We then plotted the simulated data against the observed data to graphically inspect the fit of each model (Appendix D).

4.3 RESULTS

The use of social information by American redstarts

In total, 68% (13/19) of the pre-breeding location cue treatment points were settled by ≥ 1 redstarts, compared to 15% (3/20) of the post-breeding public information points and 16% (5/30) of the control points. After controlling for the effects of habitat structure, the *settlement* model indicated that the probability of settlement at points that received the pre-breeding location cue treatment (0.71, 95% credible interval (CI) $= 0.49 - 0.89$) was

$\sim 5x$ higher than at points receiving the post-breeding public information treatment (0.15, 95% CI = $0.039 - 0.32$) and control points (0.14, 95% CI = $0.035 - 0.31$; Figure 7). The 95% credible intervals for the posterior distributions of the difference in settlement probabilities (on the *logit* scale) did not overlap zero, indicating that these differences were significant (pre-breeding location cues vs. post-breeding public information: mean= 3.06, 95% CI = $1.39 - 4.95$; pre-breeding location cues vs. control: 3.14, 95% CI = $1.41 - 5.11$). In contrast, the probability of settlement did not differ between post-breeding public information and control points (post-breeding public information vs. control: 0.075, 95% CI = $-1.75 - 1.91$; Figure 7). The difference in probability of settlement between treatments was similar for both adults and yearlings (Figure 7), indicating that both age classes responded to pre-breeding location cues, but not post-breeding public information. Although the probability of settlement was higher in 2012 than in 2013 ($\beta_3 = -1.12$), the difference was not significant (95% CI = $-2.64 - 0.29$).

Over both years of the experiment, only two redstarts were recorded at post-breeding public information points during the playback period. The number of prospectors recorded at post-breeding public information points did not differ from the number recorded at control points ($n = 1$, $z = 0.566$, $df = 1$, $p = 0.57$). These results are consistent with the lack of settlement at post-breeding public information points and together with the prospecting and settlement data confirm that redstarts did not respond to our post-breeding public information treatments.

Although the *settlement* model indicated that pre-breeding location cue treatments were the primary cue influencing redstart settlement, we also found a strong influence of habitat structure (Table 2), although adults and yearlings responded to habitat features differently (Figure 8). For adults, settlement probability was negatively correlated with habitat PC1 ($\beta_4 = -0.93$, 95% CI $= -1.66 - -0.24$) but not with the remaining habitat components (Table 2). Factor loadings indicate that the first principle component axis (PC1) was positively correlated with the number of trees and negatively correlated with shrub cover (Table D1), indicating that adult redstarts preferred sites with few trees, and to a lesser extent high shrub cover. Examination of the relationship between adult settlement probability and habitat structure indicate that the number of trees surrounding points was negatively correlated with settlement probability (estimate $\pm SE = -0.19 \pm 0.10$, $z = -1.93$, $p = 0.054$; Figure 9a).

In contrast, yearling settlement was negatively correlated with habitat PC2 ($\beta_5 = -0.82$, 95% CI $= -1.52 - -0.18$) but not the other habitat components (Table 2; Figure 8). PC2 was positively correlated with the number of saplings and negatively correlated with mean tree basal area and percent canopy cover (Table D1), indicating that yearlings chose sites that had higher tree basal area, and to a lesser extent higher percent canopy cover and fewer saplings. Examination of the relationship between yearling settlement probability and habitat structure confirm that the mean tree

basal area was positively correlated with settlement probability (389.57 ± 178.92, $z = 2.177$, $p = 0.029$; Figure 9b).

The influence of long-distance dispersal on the use of social information

Because we did not see a response to the post-breeding public information treatment, we restricted our analysis of long-distance dispersal to individuals that settled in response to pre-breeding location cues. The age ratio of yearlings to adults in the experimental group (1.5 yearlings/adult) was similar to the age ratio of individuals sampled from the general population (1.42 yearlings/adult), allowing us to directly compare immigration rates without correcting for potential age-related biases. When immigrants were classified using a 4:1 odds ratio, the immigration rate for individuals that were captured at pre-breeding location cue points (n = 15) was significantly higher than the immigration rate in the general population (n = 97; p_{diff} = 0.21, 95% CI = $0.00037 - 0.44$; Figure 10). However, the immigration rates did not differ when dispersal status was classified using the more stringent 9:1 odds ratio (p_{diff} = 0.055, 95% CI = $-0.10 - 0.27$) or the 19:1 odds ratio (p_{diff} = -0.0014, 95% CI = $-0.09 - 0.15$).

4.4 DISCUSSION

At the beginning of the breeding season, male migratory birds are under severe time constraints to locate suitable habitat and establish territories. These tasks are made more challenging because the features that influence

fitness (e.g. vegetation features, resource abundance, predation) are often not apparent at the time when settlement decisions are made. Under these circumstances, both pre-breeding location cues and post-breeding public information may provide reliable information for quickly locating suitable breeding sites but little is known about the relative importance of these cues in wild populations. Overall, our experiment demonstrates that both adult and yearling American redstarts select breeding sites based on a combination of pre-breeding location cues observed during the spring arrival period and habitat features but not based on public information gathered during the post-breeding period.

The positive response that we observed in yearlings towards pre-breeding location cues contrasts with earlier research on redstarts which found that adults, but not yearlings, responded to this source of social information (Hahn and Silverman, 2006). However, in that study, playback was broadcast on plots already occupied by redstarts whereas we purposefully placed our experimental treatments in locations that were uninhabited by redstarts. Yearling redstarts begin to arrive on the breeding grounds 7-10 days after adults (Hahn and Silverman, 2006, Rushing et al. unpubl. data) and are generally subordinate to adults when selecting breeding sites (Sherry and Holmes, 1997). Therefore, the presence of early-arriving adults on the plots used by Hahn and Silverman (2006) may have prevented yearlings from settling in response to their playback treatments. Yearlings responding to our treatments did not encounter this competition from adults and therefore were free to settle in response to our treatments.

Our results support our prediction that post-breeding public information is not an important cue for breeding site selection by yearling redstarts. As

stated above, the single synchronous brood produced by redstarts perhaps limits the availability of this social information for young individuals compared to species that have multiple broods per season. This conclusion is in line with the results of Nocera et al. (2006), who found that location cues were the primary source of social information for yearling bobolinks (*Dolichonyx oryzivorus*), another songbird with a short, synchronous breeding period. Thus, breeding synchrony and the number of broods produced within a breeding season appear to be important drivers of social information use by songbirds breeding for the first time.

In contrast, our prediction that adult redstarts would settle in response to the post-breeding public information treatments was not supported by our results. The lack of response to post-breeding public information treatments was particularly surprising given that the use of public information by adults has been documented in a number of other migratory songbirds (Boulinier and Danchin, 1997; Reed et al., 1999), including the closely related black-throated blue warbler (Betts et al., 2008). Although many of these species breed asynchronously or produce multiple broods each year, post-breeding public information should still be available to single-brooding species if failed breeders have the opportunity to observe the reproductive performance of successful individuals (Doligez et al., 2004). In our population of redstarts, 40-60% of yearling males do not acquire a mate (C. Rushing *in prep*) and public information from the territories of successful adults should be available to these individuals. The fact that they do not use this reliable source of information therefore appears toconflict with conventional research on the use of social information by migratory birds.

Although pre-breeding location cues alone may be less reliable than post-breeding public information, our results indicate redstarts of both age classes modify the use of location cues based on specific habitat features. The two habitat features identified as important drivers of settlement (tree number for adults and mean tree basal area for yearlings) are readily apparent at the beginning of the breeding season and if these features are indicative of habitat quality, combining location and habitat cues could provide an efficient and reliable method for selecting high-quality breeding sites (Szymkowiak, 2013). This strategy may be particularly important for individuals attempting to breed for the first time or in unfamiliar locations due to the lack of public information available to these individuals.

The use of stable hydrogen isotopes further allowed us to test our prediction that immigrants rely more heavily on pre-breeding location cues than philopatric individuals. When dispersal status was classified using a 4:1 odds ratio, our data indicate that the individuals that responded to pre-breeding location cue treatments were more likely to be immigrants than individuals from the general population. Furthermore, the immigration rate of the experimental group (35.3%) was high compared to immigration rates reported for other songbirds (e.g., Hansson et al., 2002; Abadi et al., 2010), including estimates based on hydrogen isotopes (Studds et al., 2012; van Wilgenburg et al., 2012), suggesting that this group was disproportionately composed of long-distance dispersers. However, when dispersal status was classified using the more conservative 9:1 and 19:1 odds ratios, the immigration rate did not differ between pre-breeding location cue treatments and the general population. Thus, although our data provide some evidence that immigrants were more likely to use pre-breeding location cues, we were not

able to conclusively accept or reject our prediction about the role of dispersal.

The inconclusive results of our dispersal analysis are likely related to several limitations of our methods that have made it difficult for us to detect an effect of dispersal on the use of social information. First, the geographic resolution of stable isotopes is low and therefore many of the individuals that were classified as local may have been short-distance dispersers that were using pre-breeding location cues. Second, although stringent thresholds (e.g. 9:1 and 19:1) make it less likely that local individuals will be misclassified as dispersers, increasing the threshold also makes the groups appear more similar, since a larger proportion of individuals in both groups will be classified as local. As a result, even if the immigration rates in the experimental group and general population differed, the more stringent thresholds may have falsely indicated that the two groups were similar. Finally, the general population almost certainly contained individuals that used location cues to select breeding sites, adding to the difficultly of detecting differences from our experimental group. Ideally, the birds that responded to our location cue treatments would be compared to a true control group made up of individuals that used a different strategy for selecting breeding sites. Unfortunately redstarts did not settle at our control or post-breeding public information points, making such a comparison impossible. Given the large difference observed under the 4:1 odds ratio, and the limitations associated with the more stringent thresholds, we suggest that our data provide at least moderate support for the prediction that long-distance dispersers rely on pre-breeding locations cues to select breeding sites to a larger extent than philopatric individuals.

Collectively, if selection favors this location/habitat cue strategy for first-time breeders and long-distance dispersers, there may be little need to develop an alternative public information-based strategy for future breeding attempts, particularly if individuals can supplement social information with personal information gained through reproductive experience. Unfortunately, it remains unknown whether this joint location/habitat cue strategy represents a viable alternative to the use of public information, largely because few studies have simultaneously compared the use of location cues and public information within the same species (Doligez et al., 2004; Nocera et al., 2006) or directly tested how the use of social information is modified by biotic and abiotic conditions (Fletcher, 2007; Betts et al., 2008).

Advancing this subject through experimental studies that simultaneously test the relationship between social information use and habitat quality is critical to predicting the vulnerability of species to changes caused by anthropogenic activities. Given that post-breeding public information is generally a reliable indication of breeding site quality, conventional wisdom holds that species that rely on public information should be less vulnerable to non-ideal habitat selection than species that rely on location cues (Doligez et al., 2003). Ironically however, precisely because public information is reliable, species that rely heavily on public information may use these cues at the expense of directly assessing habitat features. Indeed, several studies on breeding site selection in migratory birds have found that experimental simulation of social information during the post-breeding period can trump habitat cues, leading individuals to settle in suboptimal habitat (Nocera et al., 2006; Betts et al., 2008). For this reason, species that rely heavily on public information may be particularly vulnerable when anthropogenic

activities make environmental conditions less predictable. In contrast, because the presence of conspecifics can more easily become decoupled from habitat quality (Schlaepfer et al., 2002), species that rely heavily on location cues may retain the ability to directly assess habitat quality as a safeguard against selecting unsuitable breeding sites (Szymkowiak, 2013). If true, these species may be more resilient in the face of changing conditions than species that rely on public information, although more work is needed to determine the generality of these results.

Coefficient	Mean	SD	2.5% CI	97.5% CI
Total				
Control	-1.55	0.72	-2.94	-0.14
Public Information	-1.47	0.73	-2.84	-0.19
Location Cues	1.59	0.67	0.15	3.01
Year	-1.13	0.74	-2.62	0.31
Habitat PC_1	-0.85	0.30	-1.44	-0.25
Habitat PC_2	-0.77	0.32	-1.39	-0.16
Habitat PC_3	-0.16	0.33	-0.80	0.49
Adults				
Control	-2.41	0.84	-4.10	-0.79
Public Information	-4.67	1.66	-8.15	-1.83
Location Cues	1.27	0.80	-0.25	2.95
Year	-1.36	0.92	-3.19	0.48
Habitat PC_1	-0.93	0.37	-1.66	-0.24
Habitat PC_2	-0.59	0.36	-1.31	0.11
Habitat PC_3	0.29	0.37	-0.43	1.02
Yearlings				
Control	-2.12	0.77	-3.63	-0.66
Public Information	-1.72	0.65	-3.00	-0.45
Location Cues	0.54	0.66	-0.77	1.81
Year	-0.84	0.71	-2.22	0.54
Habitat PC_1	-0.27	0.25	-0.72	0.24
Habitat PC_2	-0.82	0.34	-1.52	-0.18
Habitat PC_3	0.28	0.35	-0.38	0.99

Table 2: Parameter estimates from the settlement model, including the upper and lower bounds of the 95% credible interval (CI). Interpretation of coefficients are provided in the *Analysis* section.

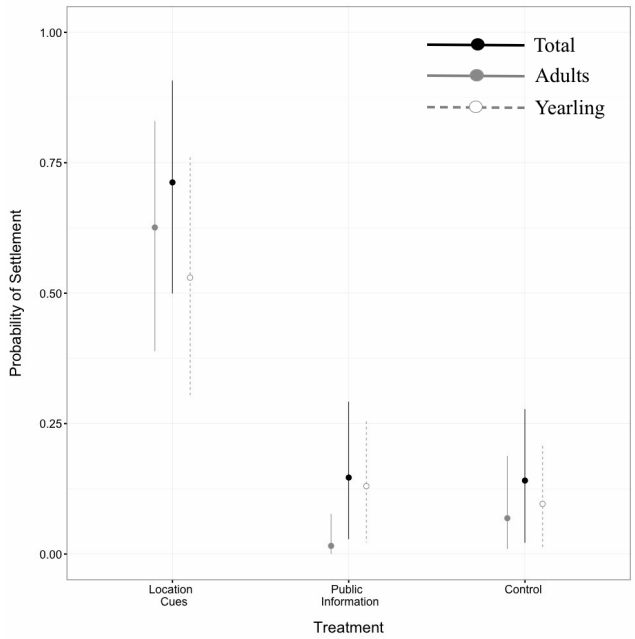


Figure 7: Response of American redstarts to experimental playback treatments. Points show the posterior means from the settlement model and error bars indicate the 95% CI for each parameter. The total response (adults and yearlings) is shown in black. Responses for adults and yearlings are shown by the gray and dashed lines, respectively. Model results indicate that, for both adults and yearlings, the probability of settlement at location cue points was significantly higher than at post-breeding public information or control points.

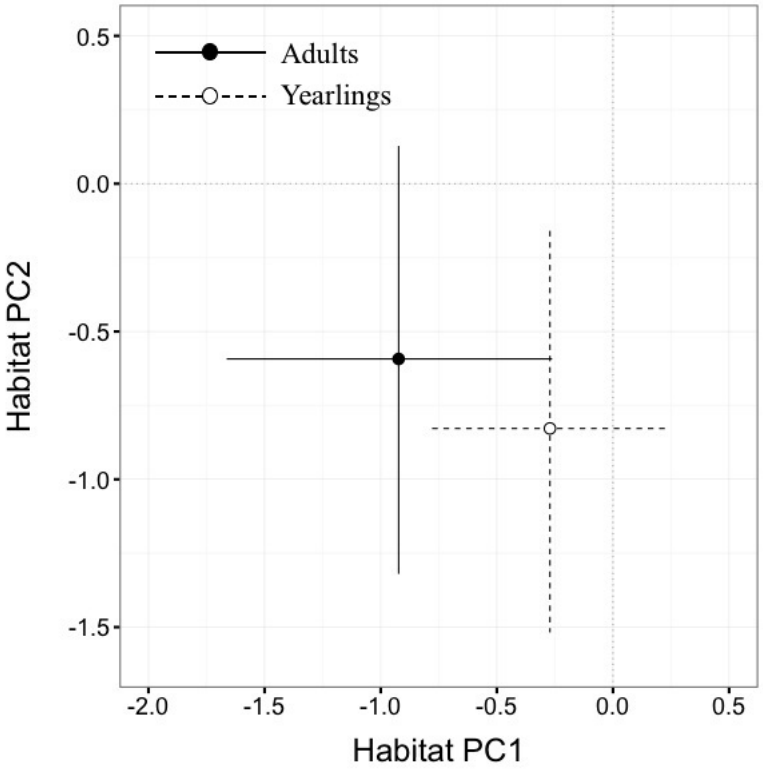
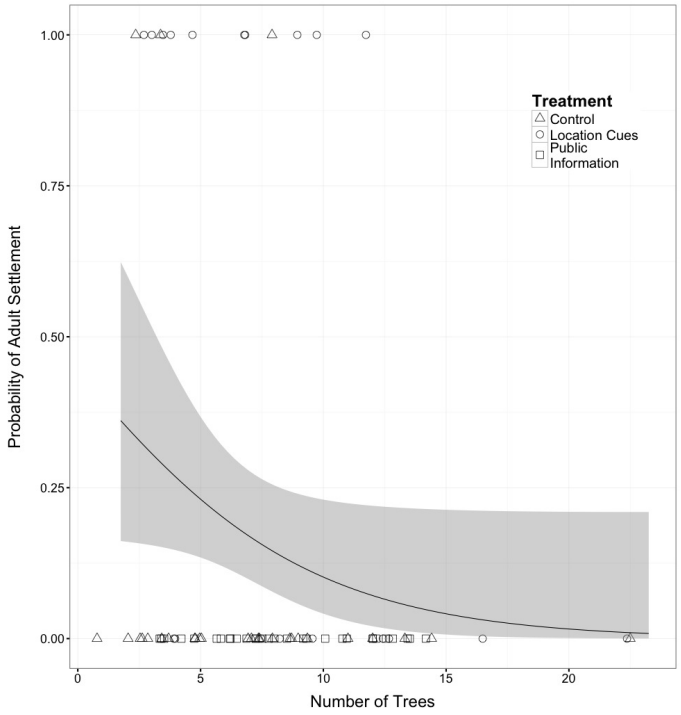
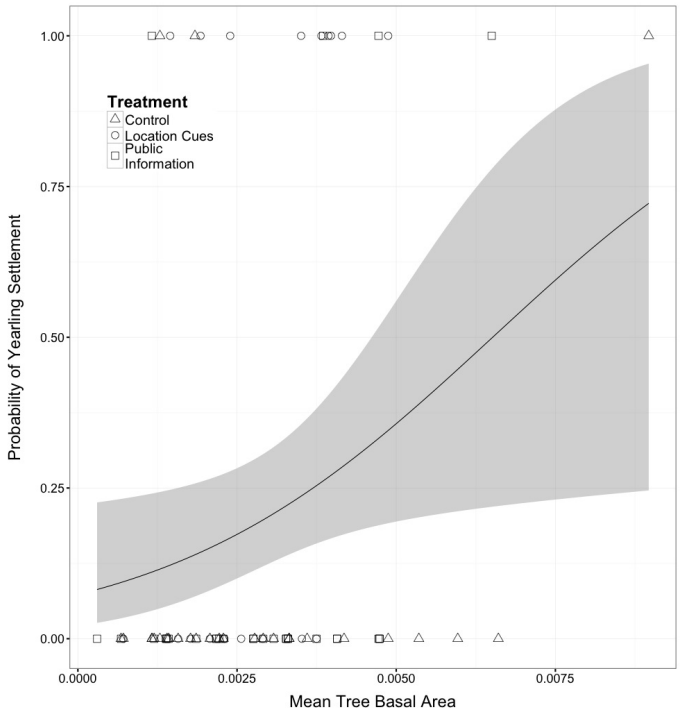


Figure 8: Response of adult and yearling redstarts to habitat structure at experimental treatment locations. Dots show the posterior means for the effects of habitat PC1 and PC2 from the settlement model. Bars show the 95% CI. For adults, the posterior mean for PC1 was negative and the 95% CI did not overlap zero, indicating that adults preferred breeding sites with a large number of beech trees and low shrub cover. For yearlings, the posterior mean for PC2 was negative and the 95% CI did not overlap zero, indicating that yearlings selected breeding sites with a large number of saplings and less canopy cover. See Appendix B for description of habitat loadings from the PCA.



(a)



(b)

Figure 9: Influence of habitat structure on the settlement probability of (a) adult and (b) yearling redstarts. Settlement of adults was influenced by the number of trees surrounding each point, with individuals selecting sites with fewer trees regardless of social information treatment. In contrast, yearlings selected sites with higher mean tree basal area.

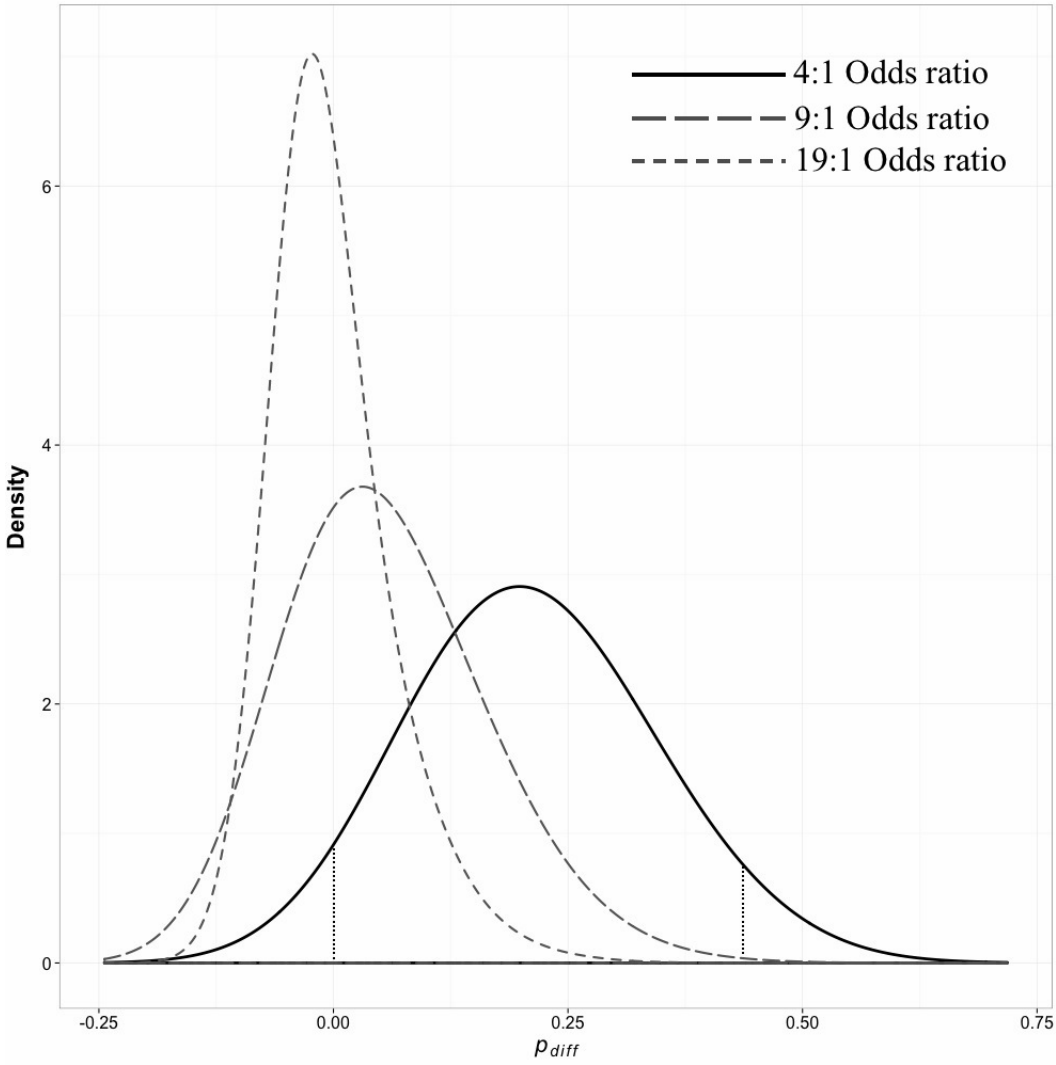


Figure 10: Posterior distributions for difference in the immigration rate (p_{diff}) between individuals that settled in response to location cue treatments and individuals from the general population. When immigrants were classified using the 4:1 odds ratio, individuals that settled in response to experimental pre-breeding location cues were more likely to be immigrants than individuals in the general population and the 95% credible interval, indicated by the vertical dotted lines, did not contain zero. However, immigration rates did not differ under the 9:1 odds ratio or the 19:1 odds ratio. The 95% CI's for the 9:1 and 19:1 odds ratio are not shown to reduce clutter.

5

DISENTANGLING THE REPRODUCTIVE CONSEQUENCES OF LONG-DISTANCE DISPERSAL AND NON-BREEDING HABITAT QUALITY IN A MIGRATORY BIRD

ABSTRACT

All environments are subject to temporal fluctuations in biotic and abiotic conditions. When these changes occur within the lifetime of individual organisms, long-distance dispersal may play a key role in synchronizing reproductive activities with conditions that maximize reproductive success. Recent work on migratory birds has demonstrated that individuals select breeding sites in response to climatic conditions but it remains unknown whether these long-distance dispersal movements carry reproductive costs that outweigh the benefits of avoiding phenological mismatches. Furthermore, because reproductive success in these species is influenced by habitat quality experienced during the non-breeding period, disentangling the influence on these carry-over effects is critical to understanding whether long-distance dispersal represents a viable mechanism for responding to fluctuations in resource phenology. In this study, we simultaneously quantify the reproductive consequences of long-distance dispersal and non-breeding territory quality in a migratory bird, the American redstart (*Setophaga ruticilla*), using a combination of stable isotope analysis and Aster life-history models. Although we predicted that long-distance dispersal would carry reproductive costs, we found no evidence that long-distance dispersers suffered lower reproductive success than philopatric individuals. However, male

reproductive success was strongly influenced by carry-over effects from the non-breeding season. For adult males, non-breeding territory quality influenced the number of young produced, but had no influence of mating or nesting success. For yearling males, in contrast, high-quality non-breeding territories were associated with higher mating and nesting success but once these differences were accounted for, non-breeding territory quality had no further influence on reproductive success. These results suggest that long-distance dispersal may be an effective strategy for responding to temporal variation in breeding habitat quality but that reproductive success in migratory birds may ultimately be limited by the quality of non-breeding habitat.

5.1 INTRODUCTION

All environments on earth are subject to temporal fluctuations in biotic and abiotic conditions. When these changes occur within the lifetime of individual organisms, such shifts in environmental conditions can negatively impact important life-history events, including survival and reproduction (Parmesan et al., 2000). Traditionally, empirical research on the response of individual organisms to changing conditions has focused on the ability of individuals to cope with changes *in situ* via phenotypic plasticity (e.g. Chown et al., 2007; Charmantier et al., 2008; Nicotra et al., 2010). However, when fluctuations in abiotic conditions are large in magnitude or occur quickly, the adaptive potential of organisms may be quickly exhausted (Both and Visser, 2001; Jump and Penuelas, 2005; Chevin et al., 2010), resulting

in individuals that are maladapted to local conditions (Post et al., 2008; Visser, 2008).

Under these circumstances, mobile individuals may alternatively track suitable conditions via long-distance dispersal. By allowing individuals to match reproductive efforts with optimal environmental conditions, long-distance dispersal can be an effective mechanism for rapidly coping with large-scale fluctuations in environmental conditions (McPeek and Holt, 1992). However, because individuals are forced to breed in unfamiliar locations, long-distance dispersal may also carry reproductive costs that could outweigh the benefits of avoiding mismatches between reproductive effort and local conditions (Bonte et al., 2012). Unfortunately, given the logistical difficulties associated with studying long-distance dispersal in the field (Koenig et al., 1996), only a few empirical studies have documented long-distance dispersal in response to fluctuations in abiotic conditions (Studds et al., 2008; Pärn and Saether, 2012; Husek et al., 2014) and estimates of the reproductive consequences of these responses are currently lacking.

In recent years, migratory birds have emerged as an ideal system to study the interaction between long-distance dispersal and temporal fluctuations in environmental conditions. In many of these species, reproductive efforts are timed to coincide with the brief but intense pulse of insect abundance that occurs in temperate regions each spring (e.g. Perrins and McCleery, 1989). Individuals that arrive on the breeding grounds too early or too late may suffer reduced survival or reproductive success (Both and Visser, 2001) because of late winter storms or because they have missed the peak in food abundance. However, because the timing of food resource phenology can vary substantially from year-to-year (Townsend et al., 2013), individuals

that remain faithful to a particular breeding location face the risk of breeding at sub-optimal times in years with abnormally early or late resource phenology (Both and Visser, 2001). Recent research suggests that, rather than suffer the reproductive consequences of these phenological mismatches, individuals of several migratory bird species may use environmental conditions experienced during migration to select breeding sites. Studds et al. (2008) used stable hydrogen isotopes to demonstrate that juvenile American redstarts (*Setophaga ruticilla*) that departed early from their non-breeding grounds tended to breed at southerly latitudes while later departing individuals bred at more northerly latitudes, consistent with the hypothesis that individuals use phenological cues to select breeding sites. These results were corroborated by the results of Chapter 3, where I show that immigrants in our breeding population of redstarts were largely of southerly origins in years with early phenology but originated from the north in years with late phenology. Similar patterns have also been observed in European populations of Pied flycatchers (*Ficedula hypoleuca*), with large influxes of morphologically-distinct southern immigrants in years with abnormally early spring phenology (Sirkiä et al., 2013) and later migrating males more likely to disperse north than early migrating individuals (Husek et al., 2014). Collectively, these results suggest that flexible long-distance dispersal behaviors may be a mechanism for synchronizing reproductive efforts with optimal environmental conditions.

However, for this strategy to be viable, the benefits of avoiding phenological mismatches must outweigh the costs of dispersing to novel breeding sites (Bonte et al., 2012). Previous studies did not report the reproductive success of immigrant and philopatric individuals, thus it remains unknown

whether the observed long-distance dispersal movements carried any reproductive costs. However, direct comparison of immigrants and philopatric individuals may be problematic because reproduction is a complex process that is influenced by a number of factors other than long-distance dispersal, including individual-level traits (e.g. age, sex, body condition: Lozano et al., 1996), biotic and abiotic conditions (Townsend et al., 2013), and trade-offs between life-history strategies (Streby et al., 2013). In empirical studies, it is often difficult to disentangle the role of these factors, particularly when they are experienced before individuals return to the breeding grounds. For example, previous work on American redstarts demonstrated that individuals holding non-breeding territories in mesic, high-quality habitat maintain body mass throughout the winter and depart earlier on spring migration than individuals forced into more xeric, low-quality habitat (Marra et al., 1998; Studds and Marra, 2005). As a result, adults from high-quality non-breeding habitat arrive earlier on the breeding grounds (Marra et al., 1998) and produce more fledglings (Reudink et al., 2009a) than adults from low-quality habitat. Given the strength of these carry-over effects from the non-breeding season, disentangling their influence on reproductive success from the influence of breeding-ground events is critical to understanding whether long-distance dispersal represents a viable mechanism for responding to temporal fluctuations in resource phenology.

In this study, we used stable hydrogen and carbon isotopes to estimate long-distance dispersal events and non-breeding territory quality, respectively, and we used Aster life-history models (Geyer et al., 2007) to quantify the influence of these factors on reproductive success. This approach allowed us to test the following specific predictions:

1) *Long-distance immigrants have lower reproductive success than local individuals:* Previous studies on long-distance dispersal in migratory songbirds have found that dispersers often suffer reduced reproductive success compared to philopatric individuals (e.g. Bensch et al., 1998; Hansson et al., 2004; Shutler et al., 2003). Therefore, we predicted that immigrants in our population would produced fewer offspring that philopatric individuals.

2) *Yearlings and adults that hold high-quality non-breeding territories have higher reproductive success than individuals from poor-quality non-breeding territories:* Previous research on American redstarts has shown that non-breeding territory quality strongly influences adult reproductive success (Marra et al., 1998; Norris et al., 2004; Reudink et al., 2009a). The reproductive consequences of non-breeding territory quality have not been well-studied with regards to yearlings but we predicted that the number of offspring produced by individuals of both age classes would be positively correlated with non-breeding territory quality.

3) *Female redstarts in good body condition have higher reproductive success than females in poor body condition:* Previous research on American redstarts has demonstrated that body condition influences the number of offspring produced by females but not males (Smith and Moore, 2003). Therefore, we predicted that the reproductive success of females in our population would be positively correlated with body condition.

4) *Adults of both sexes have higher reproductive success than yearlings*: Prior research has shown that reproductive success typically increases with age in many bird species, including redstarts (Lozano et al., 1996). Therefore, we predicted that adults would produce more offspring than yearlings.

In addition to testing these predictions, the use of Aster models allowed us to disentangle the relative influence of long-distance dispersal and non-breeding territory quality on the reproductive success of individuals in our population and to determine which reproductive components (i.e., mating success, nesting success, or the number of fledglings) drove differences in overall reproductive success. This approach provided novel mechanistic insights into the factors that determine reproductive success in this species.

5.2 METHODS

Study Species and Study Site

From 2009-2012, we studied American redstarts breeding at the Patuxent Research Refuge in Laurel, MD ($39^{o}04$'N, $76^{o}47$'W). American redstarts are long-distance Neotropical migratory songbirds that breed throughout North America and winter in the Caribbean and Latin America (Sherry and Holmes, 1997). The 250ha study area consists primarily of beech-dominated bottomland forests adjacent to the Patuxent River. Dominant tree species at the site include American beech (*Fagus grandifolia*), American elm (*Ulmus americana*), Tuliptree (*Liriodendron tuipifera*), sweetgum (*Liquidambar styraciflua*) and several species of oak (*Quercus* sp.). Understory species include American hornbeam (*Carpinus caroliniana*), Pawpaw (*Asimina triloba*) and several species of maple (*Acer* sp.).

Field Methods

Each year, the site was surveyed every three days to record the arrival date of all males breeding on the study plots. For further details about the survey and banding protocols, see Section 3.2. After banding, the territory of each male was surveyed every three days to determine whether the individual attracted a female. Males were considered to be mated if a female redstart was observed on the individual's territory and if mating behaviors (e.g. mate guarding, courtship songs, copulation, or nest building) were observed. For all territories that contained a mated pair, we searched extensively to locate all nesting attempts and monitored nests every three days until either the nest failed or nestlings were observed. Nests that were lost to abandonment, predation, weather, or otherwise produced no fledglings were considered unsuccessful. Once nestlings were observed in a nest, the nest was monitored daily until the nestlings fledged, at which time we recorded the number of fledglings. Redstarts are obligate single brooders (Sherry and Holmes, 1997), so once a nest had successfully fledged young, the adults were no longer monitored. This sampling protocol allowed us to record the status of three separate components of reproduction for each individual: 1) mated status (i.e. mated vs. unmated); 2) if mated, the fate nesting attempts (successful or unsuccessful); and 3) if a nesting attempt was successful, the number of fledglings produced.

Quantifying the factors that influence reproductive success

To avoid testing a large number of models that had little biological justification, we focused our analysis on factors known a priori to influence reproductive success of American redstarts or closely related species. This approach allowed us to quantify and disentangle the influence of the following factors:

1) Dispersal Status:

To estimate the dispersal status of individuals in our population, we used to stable hydrogen isotopes from feather samples ($\delta^2 H_f$) to probabilistically determined the origin of all unknown-origin individuals in our population (van Wilgenburg et al., 2012). See Section 3.2 and Appendix B for further details about inferring dispersal status. To test the sensitivity of our results to the threshold used to classify dispersal status, we carried out the classifications and statistical analyses using two progressively stringent thresholds (4:1 odds and 9:1 odds). To account for both age-specific consequences and annual variation in reproductive consequences, we included the interactions of dispersal status with both age class and year in our analysis.

2) Non-breeding territory quality:

To infer non-breeding territory quality, we used stable carbon isotope values from claw samples ($\delta^{13}C$). Details about the use of $\delta^{13}C$ to infer non-breeding territory quality can be found in Section 3.2. To aid in interpretability, we mean-centered $\delta^{13}C$ so that positive values indicate higher than aver-

age habitat quality and negative values indicate lower than average quality and we included the interaction of $\delta^{13}C$ with age class in our analysis to account for age-specific effects of non-breeding territory quality.

3) Body condition:

To test our prediction about the influence of body condition on reproductive success, we estimated the body condition of all individuals in our analysis following the methods described in Section 3.2. To reduce the number of parameters in our models, and because previous research on American redstarts has demonstrated that body condition influences the reproductive success of females but not males (Smith and Moore, 2003), body condition (and its interaction with age class) was only included in the analysis of female reproductive success.

4) Year and age effects:

Reproductive success typically increases with age in many bird species, including redstarts (Lozano et al., 1996), and populations of many songbirds show substantial annual variation in reproductive success (Townsend et al., 2013). To account for annual variation not accounted for by other predictors, we included year effects in all models.

As described above, arrival date on the breeding grounds is highly correlated with reproductive success in redstarts (Marra et al., 1998). However, because the arrival date of males in our population was significantly correlated with $\delta^{13}C$ values (Pearson's correlation coefficient = -0.249, t = -3.491, $P < 0.001$) and because we are confidant of the causal relationship between these variables (non-breeding habitat quality drives arrival date and not

vice versa), we chose to omit arrival date from our analysis to avoid the co-linearity caused by this correlation.

Statistical Analysis: Aster life-history models

In many songbird species, the distribution of reproductive success is bimodal (e.g. Lozano et al., 1996), with a structural mode at zero (corresponding to individuals that either failed to acquire a mate or to nest successfully) and a second mode corresponding to the mean number of fledglings for individuals that mated and nested successfully. This mixture of discrete and continuous components is typical of life-history data (Shaw et al., 2008) and presents several challenges for analysis. First, the joint distribution of the individual reproductive components (i.e. mating success, nesting success, and number of fledglings) does not follow any standard parametric distribution and therefore violates the assumptions of standard generalized linear models (Geyer et al., 2007). Second, although modeling each reproductive component separately can overcome the first limitation, independent analysis of each component decreases the sample size for later components (because individuals that failed at earlier stages must be removed, Geyer et al., 2007) and prevents conclusions about overall reproductive success (Shaw et al., 2008).

Aster modeling (Geyer et al., 2007) is a recently developed method for analyzing life-history data that overcomes the challenges presented by data of this nature. Aster models allow the joint distribution of response variables (i.e. components of reproductive success) to be modeled as the prod-

uct of conditional distributions and thus directly account for the conditional nature of reproductive data (Geyer et al., 2007). Furthermore, each component can follow any exponential-family distribution, which includes most standard distributions used to analyze reproductive data. A simple graphical model is used to describe the conditional relationships between the reproductive components (Figure 11a), with arrows pointing from earlier components (i.e. predecessor nodes) to later components (i.e. successor nodes; Shaw et al., 2008). Because the effects of predictor variables on successor nodes are propagated back through each predecessor node (Shaw et al., 2008), Aster models allow researchers to quantify the effects on overall reproductive success while directly accounting for the contributions of each reproductive component.

For our analysis of reproductive success, we used unconditional Aster models (Geyer et al., 2007) and considered mated success and nesting success to be Bernoulli trials and the number of fledglings to follow a 0-truncated Poisson distribution (Figure 11a). To test the predictions outlined above, we first fit a 'full' model that contained explicit effects of all predictors on the number of fledglings produced by each individual. But as described, due to the conditional nature of Aster models, the estimates for each predictor propagate back through predecessor nodes and thus directly account for differences due to mating and nesting success (Geyer et al., 2007). Because the reproductive success of individuals from mated pairs cannot be considered independent, we fit separate models for males and females. To test the significance of each predictor, we dropped the predictor from the 'full' model and then tested the fit of the reduced model using a likelihood ratio test (Nevoux et al., 2013). For predictors that were included in inter-

action terms, main effects were tested by dropping both the main effect and interactions. To test the sensitivity of our results to the threshold used to classify dispersal status, the models without dispersal status were compared to "full" models based on both the 4:1 and 9:1 odds ratios. All models were fit using the "aster" package (Geyer, 2012) in the R statistical language (R Core Team, 2013).

Which reproductive components drive reproductive differences?

Although our primary interest was in quantifying the factors that influence overall reproductive success (i.e. the number of fledglings), determining which reproductive component(s) drive the variation in reproductive success can provide important mechanistic insights into processes that influence reproduction. For example, long-distance dispersal may be costly because females choose to mate with males with similar phenotypes (Bensch et al., 1998) or alternatively because immigrants are not familiar with local habitat features (Pärt, 1990). In either case, our 'full' analysis would indicate that immigrants have lower reproductive success than local individuals even though the differences were driven primarily by mating success in the former but by nesting success in the later.

To determine which components of reproductive success were responsible for the results observed in our 'full' model, we fit additional Aster models for each predictor variable that was found to have a significant influence on overall reproductive success. The first of these 'component' models included the effects of the predictor of interest only on the probability of

mating ('mate' model) and therefore did not account for any reproductive differences caused by nesting success or the number of fledglings. The second component model contained explicit effects on nesting success ('nest' model), but due to the nature of Aster models, this model also included differences in mating success. The third component model contained explicit effects on the number of fledglings ('fledgling' model). For each component model, any additional predictors that were not of primary interest were kept as effects on the number of fledglings. We also fit a 'base' model that did not contain the effect of the predictor of interest and used likelihood ratio tests (LRT) to compare each component model to the 'base' model, with a significant LRT indicating differences in reproductive success up to that component due to the predictor of interest.

Because the 'nest' model and 'fledglings' model include the effects of earlier components, significant LRT tests when compared to the 'base' model do not indicate which components are responsible for differences in reproductive success. For example, a significant LRT for the 'nest' model could indicate that individuals have lower mating success, lower nesting success, or both. Therefore, our component analysis included two additional models that contained explicit effects on each component and its successor component (e.g. 'mate + nest' & 'nest + fledglings'). The single component models were then compared to the more complicated models using likelihood ratio tests, allowing us to determine whether adding effects on the successor components improved the fit of the single component models. This allowed us to determine which reproductive components drove differences in overall reproductive success, providing additional insights into the mechanisms by which breeding and non-breeding season processes influence reproduction.

5.3 RESULTS

What factors influence reproductive success?

Between 2009 and 2012, we monitored the reproductive success of 260 redstarts, including 63 adult males, 48 adult females, 123 yearling males, and 26 yearling females. A description of the long-distance dispersal patterns observed in this population can be found in Chapter 3. The mean number of fledglings per individual in our study population was 1.37 (± 1.48 SD; range 0-6). On average, adults had higher reproductive success than yearlings (adults: 2.27 ± 1.39 fledglings, range 0-6; yearlings: 0.61 ± 1.06 fledglings, range 0-4) and a Poisson regression indicated the difference was significant (estimate ± SE: -0.264 ± 0.122, z = -2.162, P = 0.0307). However, a large proportion of individuals in our population (47.7%) failed to produce any fledglings, resulting in a strongly bimodal distribution for the number of fledglings (Figure 11b). The distinct mode at zero was primarily the result of low mating success of yearling males (43.1%). In contrast, all females and virtually all adult males (98.4%) mated successfully. The remaining zeros were the result of individuals that failed to nest successfully and a logistic regression restricted to individuals that successfully acquired a mate indicated that yearlings of both sexes were significantly less likely to nest successfully than adults (age effect ± SE: -1.49 ± 0.358, z = -4.178, $P < 0.001$).

Although the simple *glm* models for each component of reproductive success indicated that yearlings are less successful than adults at each stage

of reproduction, the use of Aster models allowed us to quantify the overall reproductive consequences of age and the other predictor variables (Table 3). The 'full' Aster models for both males and females confirmed that yearlings had lower reproductive success than adults (Table 3), with yearling males producing on average 80% fewer fledglings than adult males (yearling males: 0.428 ± 0.0813 fledglings; adult males: 2.045 ± 0.257 fledglings) and yearling females producing on average 26% fewer fledglings than adult females (yearling females: 1.75 ± 0.291 fledglings; adult females: 2.38 ± 0.236 fledglings). The Aster analysis also revealed a strong year effect for yearling males, with higher reproductive success in 2010 and 2012 than in 2009 and 2011 (Table 3).

The role of long-distance dispersal

Although we predicted that immigrants would produce fewer fledglings than local recruits, dispersal status was not a significant predictor of reproductive success for either sex (Table 3; Figure 12) and likelihood ratio tests indicated no significant dispersal x age class interaction for either sex (males: $\chi^2 = 0.166$, *d.f.* = 2, $P = 0922$; females: $\chi^2 = 0.227$, *d.f.* = 1, $P = 0.633$). These results were not sensitive to the odds ratio used to classify dispersal status (Table 3; Figure 12). Unfortunately, we were unable to test for dispersal x year interactions due to small within year sample sizes for each dispersal category.

The role of non-breeding territory quality

In contrast, the Aster analysis revealed a significant impact of non-breeding territory quality on the overall reproductive success of males (Table 3),

confirming our prediction that individuals that held high-quality territories during the preceding winter produced more fledglings than individuals from low quality habitat (Figure 13). However, the interaction of non-breeding habitat quality and age was not significant ($\chi^2 = 0.842$, *d.f.* $= 1$, $P = 0.359$), indicating that the consequences of non-breeding habitat quality on overall reproductive were similar for both age classes. Based on estimates from the 'full' model for males, males of both age classes from the lowest quality non-breeding habitat suffered a nearly 90% reduction in reproductive success compared to individuals from the highest quality habitat (Figure 13). In contrast, and contrary to our predictions, non-breeding habitat quality did not influence reproductive success in females, nor did body condition (Table 3).

Which reproductive components drive reproductive differences?

Because we did not find evidence that non-breeding habitat quality, dispersal status, or body condition influenced female reproductive success, we limited our analysis of reproductive components to males only. Furthermore, because all but one adult male in our population acquired a mate, we restricted our adult male component analysis to nesting success and the number of fledglings.

Adult males

Based on the results of our full model for male reproductive success, our component analysis for adult males included only the influence of non-

breeding territory quality, leading to four models (Table 4). As expected, the 'fledglings' model for adult males indicated an effect of non-breeding habitat quality on the number of fledglings (Table 4: 'fledglings' model vs. 'base' model), though the improvement was only marginally significant. In contrast, comparison of the 'nest' model to the 'base' indicated that non-breeding habitat quality did not influence nesting success in adult males (Table 4: 'nest' model vs. 'base' model). This conclusion is supported by the fact that adding explicit effects on the number of fledglings significantly improved the fit of the 'nest' model (Table 4: 'nest' model vs. 'nest + fledglings' model). Thus, our results indicate the non-breeding territory quality drives variation in reproductive success of adult males by directly influencing the number of fledglings produced.

Yearling males

For yearling males, the 'full' model indicated that both non-breeding territory quality and year influenced reproductive success (Table 3). Because our primary interest was on the influence of non-breeding territory quality and not year, we fit six component models that included explicit year effects on the number of fledglings but differed in which component was influenced by non-breeding territory quality (Table 4). Comparison of the 'mate' model to the 'base' model uncovered a clear effect of non-breeding territory quality on mating success (Table 4: 'base' model vs. 'mate' model), indicating that yearling males from high-quality territories were more likely to acquire a mate than individuals from low-quality territories (Figure 14a). Adding explicit effects on nesting success further improved the fit of the model (Table 3: 'mate' model vs. 'mate + nest' model), indicating that even once the

effects of mating success are accounted for, yearling males from high-quality non-breeding territories were more likely to nest successfully than individuals from low-quality territories (Figure 14b). This conclusion is supported by the significantly better fit of the 'nest' model compared to the 'base' model (Table 4: 'nest' model vs. 'base' model). As expected, the 'fledglings' model revealed a clear impact of non-breeding habitat quality on the number of fledglings produced (Table 4: 'fledglings' model vs. 'base' model) but adding explicit effects on the number of fledglings did not improve the fit compared to the 'nest' model (Table 4: 'nest' model vs. 'nest + fledglings' model), indicating that once the effects on mating and nesting success are accounted for, non-breeding territory quality had no further influence on the number of fledglings produced by yearling males.

5.4 DISCUSSION

A small but growing number of studies indicate that migratory birds use phenological cues experienced during migration to select breeding sites (Studds et al., 2008; Husek et al., 2014, Rushing et al. in review) but whether these movements carry reproductive costs remains poorly understood. In this study, we used a combination of stable isotope analysis and novel analytical methods to disentangle the reproductive consequences of breeding-season and non-breeding season events in a migratory songbird. Contrary to our predictions, we found no reproductive costs to long-distance dispersal in either sex or age class and these results were not sensitive to the threshold used to classify dispersal status. Although these results appear to

contradict previous studies that found long-distance dispersal reduced lifetime reproductive success in several migratory bird species (Wheelwright and Mauck, 1998; Hansson et al., 2004; Nevoux et al., 2013), none of these studies found an immediate influence of long-distance dispersal on fecundity. Likewise, other studies that have measured single-season reproductive consequences of long-distance dispersal in migratory birds have also not found evidence that immigrants produce fewer fledglings than local individuals (Shutler et al., 2003). Collectively, these results indicate that long-distance dispersal does not carry immediate reproductive costs for migratory birds and suggest that the benefits of dispersing to avoid phenological mismatches may outweigh the costs of reproducing in unfamiliar locations.

However, although we did not find evidence that reproductive success differed between immigrants and philopatric individuals, it must be noted that our analysis was restricted only to individuals that had successfully dispersed. As a result, our results do not imply that long-distance dispersal is not costly with regards to overall fitness because it remains possible that long-distance dispersal may influence survival. Recent work on migratory birds indicates that the probability of surviving migration decreases with increasing migration distance (Lok et al., 2011; Sanz-Aguilar et al., 2012), suggesting that the survival costs of long-distance dispersal may be indirectly influenced by mortality experienced during migration. If true, this interaction between dispersal costs and migration distance implies that the fitness consequences of long-distance dispersal may be tightly linked to the costs and benefits of migration. As researchers seek a better and more mechanistic understanding of the consequences of long-distance dispersal in

migratory species, future research would greatly benefit from an integrated perspective that considers costs experienced during migration.

Habitat quality experienced during the preceding winter, but not long-distance dispersal, strongly influenced the reproductive success of males in our population but neither non-breeding territory quality nor long-distance dispersal influenced reproductive success in females. The influence of non-breeding habitat quality on adult male reproductive success is consistent with previous research on American redstarts (Marra et al., 1998; Norris et al., 2004; Reudink et al., 2009a) but the use of Aster models revealed novel mechanisms by which carry-over effects from the non-breeding season influence reproductive success in yearling males. For these individuals, high-quality non-breeding habitat was associated with both higher mating success and higher nesting success than low-quality habitat but once these differences were accounted for, non-breeding habitat had no further influence on the number of fledglings. Although a number of factors could explain these results, we suggest that the reproductive differences within and between age classes are due to a combination of differences in the timing of arrival on the breeding ground and individual quality (McKellar et al., 2013).

In redstarts and many other songbirds, early arrival on the breeding grounds is associated with increased access to potential mates and high-quality territories (Palokangas et al., 1992; Aebischer et al., 1996; Lozano et al., 1996), higher nesting success (Grant et al., 2005), and larger clutch size (Perrins and McCleery, 1989). Thus, non-breeding habitat may influence reproductive differences primarily by driving variation in arrival date (Marra et al., 1998). Indeed, amongst males in our population, non-breeding

territory quality was highly correlated with arrival date (Pearson's correlation coefficient = -0.249, t = -3.491, $P < 0.001$) and arrival date was a strong predictor of the number of fledglings produced (estimate ± SE: -0.603 ± 0.0661, z = -9.109, $P < 0.001$). However, if arrival timing was the primary driver of the age-specific differences revealed by our Aster analysis, than we would further predict that arrival date should be strongly correlated with mating success and nesting success for yearling males, but not for adults. However, arrival date did not predict mating success (yearlings: -0.184 ± 0.253, z =-0.727, P = 0.467; adults: no test because 98.4% of adult males were mated) or nesting success (yearlings: -0.144 ± 0.313, z = -0.460, P = 0.645; adults: 0.248 ± 0.529, z = 0.470, P = 0.638) in either age class. Thus, arrival date alone does not explain the relationship between non-breeding territory quality and reproductive success in yearling males.

An alternative to the arrival-timing hypothesis is that variation in reproductive success is determined by differences in individual quality (McKellar et al., 2013). Both within and between age classes, high-quality individuals are expected to acquire the best breeding (Leniowski and Wegrzyn, 2013) and non-breeding territories (Marra and Holmes, 2001), attract females (Lozano et al., 1996), nest successfully (Saino et al., 2012), and provide greater parental care to nestlings (Crossin et al., 2012). In our population, the higher mating success, nesting success, and total reproductive success of adult males compared to yearling males supports the hypothesis that adults are generally higher quality mates than yearlings (Lozano et al., 1996). For yearling males, the significant relationship between non-breeding territory quality and mating and nesting success (Figure 14) and the lack of relationship between arrival date and these components further supports

the hypothesis that variation in reproductive success is determined primarily by individual quality. We suggest that yearling males that were able to hold high-quality non-breeding territories are competitively dominant to the yearlings that were forced into low-quality habitat (Marra, 2000) and these high-quality individuals may be more attractive to females (Reudink et al., 2009b) and may also be better at defending nests (Kazama and Watanuki, 2010). Although our data did not allow us to further test these predictions, our results are largely consistent with the work of McKellar et al. (2013), who used experimental manipulations to show that reproductive success of adult redstarts was a function of both arrival date and individual quality.

Quantifying the reproductive consequences of long-distance dispersal and non-breeding habitat quality are critical to understanding if and how migratory species will respond to global climate change (Le Galliard et al., 2012). Although a large number of studies have focused on the impacts of advancing temperate phenology (e.g., Both and Visser, 2001; Møller et al., 2008; Saino et al., 2011), climate change is also predicted to result in decreased precipitation in many of the tropical areas inhabited by migratory birds during their non-breeding period (Neelin et al., 2006). Our results indicate that this long-term decline in non-breeding habitat quality may have a larger impact on the reproductive success of migratory birds than advances in resource phenology caused by temperate warming. While additional work is needed to fully understand the impacts of climate change on migratory birds (Knudsen et al., 2011), our results highlight the importance of accounting for the full annual cycle when considering the vulnerability of migratory birds to climate change (Small-Lorenz et al., 2013).

Variable		Estimate ± SE	z	χ^2	*d.f.*	P
Males, n = 186						
Age class		**-1.759 ± 0.639**	**-2.749**	**53.42**	**1**	**< 0.001**
Origin	Local	0.0716 ± 0.217 (-0.162 ± 0.294)	0.274 (-0.550)	1.822 (0.373)	2	0.402 (0.829)
	Southern	0.293 ± 0.341 (-0.249 ± 0.442)	-0.824 (-0.565)			
Non-breeding habitat quality		**0.419 ± 0.119**	**3.511**	**13.011**	**1**	**<0.001**
Year	2010	-0.346 ± 0.209	-1.632	2.522	3	0.4713
	2011	0.192 ± 0.221	0.872			
	2012	-0.147 ± 0.192	-0.764			
Year x Age class	**2010**	**1.386 ± 0.677**	**1.782**	**13.653**	**3**	**0.00342**
	2011	**0.0774 ± 0.717**	**0.122**			
	2012	**1.045 ± 0.659**	**1.582**			
Females, n = 74						
Age class		**-0.461 ± 0.223**	**-2.067**	**4.628**	**1**	**0.0317**
Origin	Local	0.0455 ± 0.394 (0.0337 ± 0.401)	0.127 (0.076)	0.117 (0.668)	2	0.9433 (0.716)
	Southern	-0.185 ± 0.776 (0.611 ± 0.798)	-0.241 (0.765)			
Non-breeding habitat quality		-0.00799 ± 0.191	-0.042	0.00176	1	0.967
Body condition		-0.1228± 0.184	-1.239	1.556	1	0.212
Year	2010	0.0553 ± 0.247	0.242	2.926	3	0.403
	2011	0.401 ± 0.241	1.664			
	2012	-0.0553 ± 0.235	-0.235			

Table 3: Factors influencing reproductive success in American redstarts. Coefficient estimates ± SE are from the 'full' unconditional Aster models for male and female reproductive success. $\chi 2$, d.f. and P values refer to the likelihood ratio test (LRT) test used to compare the reduced model to the full model. For dispersal status, values outside parentheses are based on the 80% threshold and values inside parentheses are based on the 90% threshold. The age class predictor and year predictors treat adults and the year 2009 as dummy variables, respectively. Interaction terms from the full model that were not significant were dropped and are not displayed here. Bold values indicate predictor variables that were significant at the 0.05 level and italics indicate variables that were significant at the 0.1 level. LRT statistics for main effects that are included in interaction terms are based on removing both the interaction and main effect from the full model.

Model	Model Deviance	Model *d.f.*	Test Deviance	Test *d.f.*	*P*
Adults, n = 63					
Base	57.891	3	-	-	-
Nest[a]	57.778	4	0.113	1	0.737
Fledglings[a]	*54.156*	*4*	*3.735*	*1*	*0.0532*
Nest + Fledglings[b]	**53.068**	**5**	**4.710**	**1**	**0.0299**
Yearlings, n = 123					
Base	258.991	6	-	-	-
Mate[a]	**253.597**	**7**	**5.394**	**1**	**0.0202**
Nest[a]	**250.071**	**7**	**8.920**	**1**	**0.00282**
Fledglings[a]	**251.049**	**7**	**7.942**	**1**	**0.00483**
Mate + Nest[c]	**249.458**	**8**	**4.139**	**1**	**0.0419**
Nest + Fledglings[b]	249.590	8	0.481	1	0.482

Table 4: Results of analysis to determine which components of male reproductive success are influenced by non-breeding habitat quality. Each model contains explicit effects on non-breeding territory quality on only the reproductive component(s) indicated by the model name. For a full description of the models, see *Methods*. Test statistics for each model show the results of a likelihood ratio test (LRT) comparing that model to a nested model that included explicit effects of non-breeding territory quality only on earlier reproductive components. A significant result indicates that the reproductive component(s) given in the name of the model were significantly influenced by non-breeding territory quality. Models shown in bold were significant at the 0.05 level and models shown in italics were significant at the 0.1 level

a Likelihood ratio test statistics indicate fit compared to 'base' model

b Likelihood ratio test statistics indicate fit compared to 'nest' model

c Likelihood ratio test statistics indicate fit to compared to 'mate' model

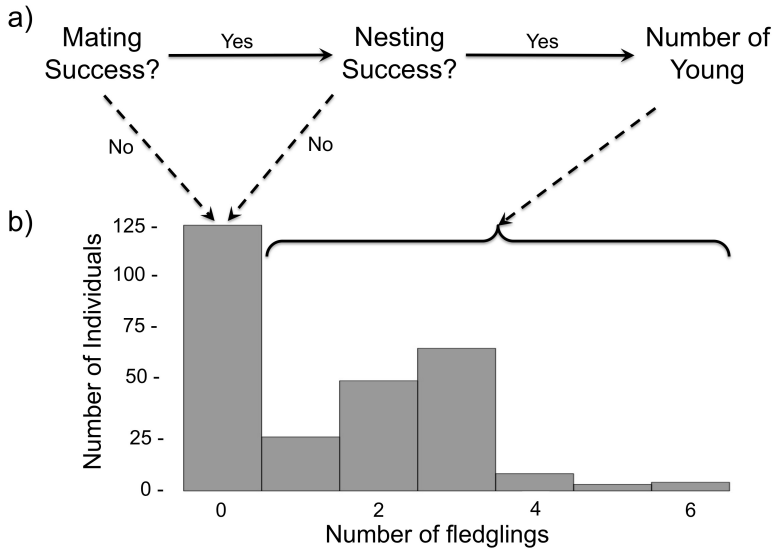


Figure 11: (a) Graphical model illustrating the relationship between components of reproductive success in our analysis, with solid arrows leading from earlier components (predecessor nodes) to later components (successor nodes). If a predecessor node equals 0 (due to failure to mate or nest successful), all successor nodes must also equal 0. In our analysis, overall reproductive success is measured as the number of young, conditional on mating and nesting successfully. Mating success and nesting success were modeled as binomial variables and the number of young was modeled as a zero-truncated Poisson variable conditional on successful mating. (b) Distribution of the reproductive success of all individuals (males and females) breeding in our study population, measured as the number of fledglings produced by each individual. The discrete mode at zero corresponds to individuals that failed to mate or that lost their nest prior to fledging, producing a distribution that does not follow any standard parametric distribution.

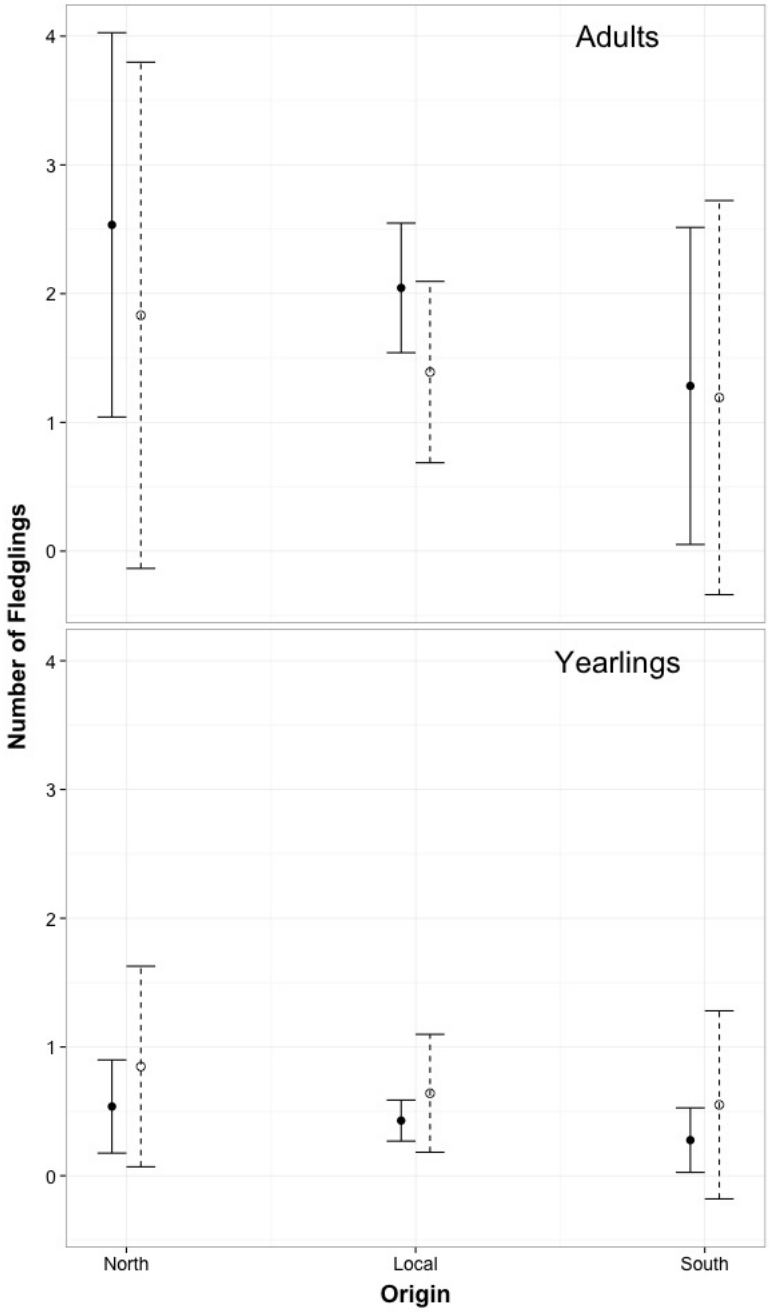


Figure 12: Predicted number of fledglings for adult (top) and yearling (bottom) males in each dispersal category based on the 'full' Aster model and assuming all other predictor variables at their mean. Closed circles and solid bars show estimates assuming a 80% threshold for classifying dispersal status, open circles and dashed bars show estimates assuming a 90% threshold. Error bars show 95% confidence interval.

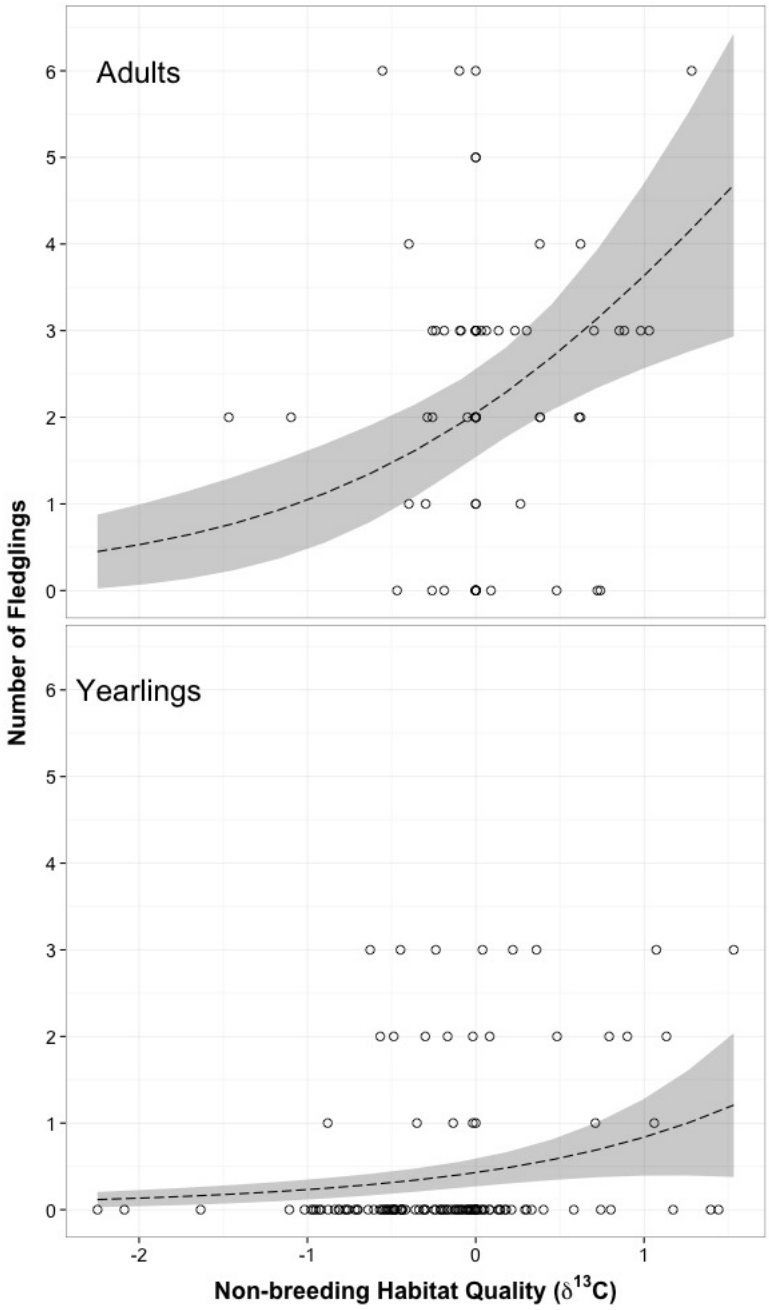
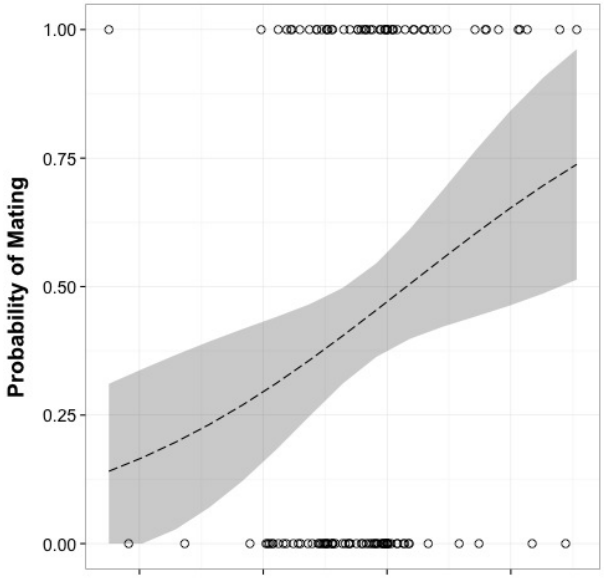
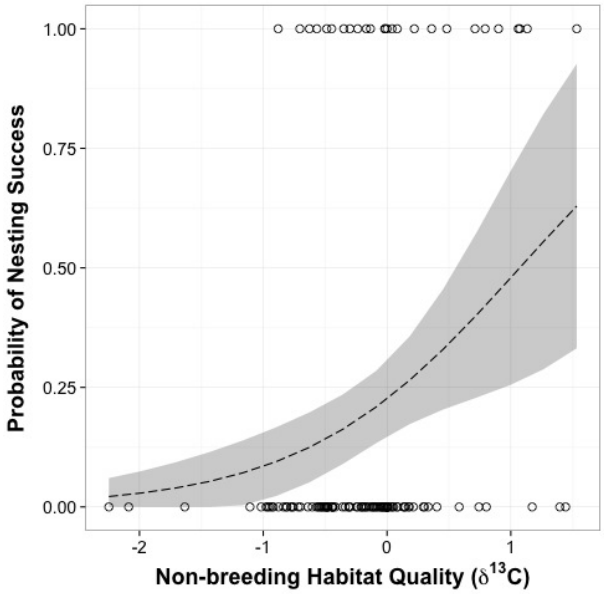


Figure 13: Predicted number of fledglings for adult (top) and yearling (bottom) males as a function of non-breeding territory quality (δ^{13}C) based on the 'full' Aster model and assuming individuals originated locally. δ^{13}C values were mean-centered previous to analysis so positive values indicate better than average non-breeding habitat quality and negative values indicate less than average habitat quality. Open circles show the actual number of fledglings for individuals in our study population. Gray ribbon show the 95% confidence interval. For both age classes, individuals that spent the preceding winter in high quality habitat tend to fledge more young than individuals from low quality habitat.



(a)



(b)

Figure 14: Probability of (a) acquiring a mate and (b) successfully nesting for yearling males as a function of non-breeding territory quality (δ^{13}C) based on the 'mate' and 'fledge' component models and assuming individuals originated locally. δ^{13}C values were mean-centered previous to analysis so positive values indicate better than average non-breeding habitat quality and negative values indicate less than average habitat quality. Open circles show the actual number of fledglings for individuals in our study population. Gray ribbon show the 95% confidence interval. Individuals that spend the preceding winter in high quality habitat are more likely to acquire a mate and to nest successfully than individuals from low quality territory.

APPENDIX A: RESULTS OF LITERATURE REVIEW

Table S1: Research on the causes of dispersal and site fidelity in migratory species during: (a) breeding season; (b) non-breeding season; (c) stopover; (d) molting. Studies that only quantify rates of site fidelity without regard to factors influencing these rates were excluded. Dispersal abbreviations: DD- dispersal distance; NDD- natal dispersal distance; BDD- breeding dispersal distance; DP- dispersal probability; SF- probability of site fidelity; GF- gene flow; Dir- dispersal direction. Factor abbreviations: Clim.- climate; Cond.- body condition; Den.- density; HQ- habitat quality; Impr.- imprinting; Par.- parasitism; Pros.- prospecting; RS- previous reproductive success; Size- body size; FD – fledgling date.

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
(a) Breeding season					
Birds					
	King eider *Somateria spectabilis*	SF	Sex	Site fidelity higher in females than in males	Phillips and Powell (2006)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Northern pintail *Anas acuta*	SF	Sex, HQ	Site fidelity higher in females than in males; Both sexes showed higher fidelity in years when habitat conditions were poor in nearby areas	Nicolai et al. (2005)
	Barnacle goose *Branta leucopsis*	DP	Sex, Size, Pros	Large males more likely to disperse between colonies than smaller males or females	van der Jeugd (2001)
	Black brandt *Branta bernicla nigricans*	SF, DP	Age, Sex	Site fidelity did not differ between adult males and adult females; site fidelity was higher in juvenile females than juvenile males	Lindberg et al. (1998)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Spotted sandpiper *Actitis macularia*	SF	Age, Sex, RS	Site fidelity was higher in juvenile females than juvenile males; No effect of sex on site fidelity for older birds; Both sexes were more likely to return after successful reproduction	Oring and Lank (1982)
	Semipalmated sandpiper *Calidis pusilla*	SF	Age, Sex	No evidence for sex differences in natal site fidelity; Individuals breeding for the first time at age bred closer to their natal site than individuals breeding for the first time at older ages	Gratto (1988)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Arctic tern *Sterna paradisaea*	NDD, BDD	Clim.	Natal dispersal distance was related to climate conditions experienced on the breeding grounds; Breeding dispersal distance was influenced by climate conditions experienced during both the breeding and non-breeding periods	Møller et al. (2006)
	Black kite *Milvus migrans*	NDD	Age, Sex, HQ, Den, Pros, Cond	Females disperse farther than males; Breeding density was negatively correlated with natal dispersal distance in both sexes	Forero et al. (2002)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Lesser kestrel *Falco naumanni*	DP	Age, Sex, RS, HQ, Den, Cond	Probability of dispersal decreased with age; Females dispersed more often than males; Dispersal probability decreased in individuals that reproduce successfully; Immigration was higher into high quality colonies, regardless of colony size	Calabuig et al. (2008)
	Swainson's hawk *Buteo swainsoni*	NDD	Sex, RS, Den, HQ	Juvenile females dispersed farther than juvenile males; Natal dispersal distance was negatively correlated with habitat quality and positively correlated with population density	Briggs et al. (2012)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Flammulated owl *Otus flammeolus*	SF	Sex, RS	Site fidelity was higher in males than females; Females that reproduced successfully more likely to return than unsuccessful females	Linkhart et al. (2007)
	Barn swallow *Hirundo rustica*	SF, NDD, BDD	Age, Sex, RS	Site fidelity was higher in adults than juveniles; Females dispersed more and farther than males; Both sexes were more likely to return after successful reproduction	Shields (1984)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Cliff swallow *Petrochelidon pyrrhonota*	NDD	Sex, Size, Par	Nestlings infected with ectoparasites were more likely to disperse to nonnatal colonies the following year than unparasitized individuals	Brown and Brown (1992)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Tree swallow *Tachycineta bicolor*	NDD/BDD	Sex, Age, RS	Adult females dispersed farther than adult males but natal dispersal distances did not differ between sexes; Dispersal distance decreased with age for both sexes; Number of siblings did not influence subsequent natal dispersal distance; Manipulating the number of eggs in nest did not influence subsequent breeding dispersal distance for either sex	Shutler et al. (2003)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
		NDD	Sex	Females dispersed farther than males; No effect of fledging date on subsequent natal dispersal distance	Winkler et al. (2005)
		BDD	Sex, RS	Females more likely to disperse than males; Females that successfully reproduced were less likely to change breeding sites the following year;	Winkler et al. (2004)
		NDD/BDD	Sex, Age	Juveniles dispersed farther than adults; Dispersal distances were similar for males and females	Hosner and Winkler (2007)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Eastern kingbird *Tyrannus tyrannus*	SF, BDD	Sex, RS	Site fidelity was higher in males than females; Females dispersed farther than males; Females that reproduced successfully more likely to return than unsuccessful females but reproductive success did not influence male site fidelity	Murphy (1996)
	Eastern phoebe *Sayornis phoebe*	BDD	Sex, RS	Dispersal distance was similar for males and females; Both sexes were more likely to disperse after unsuccessful reproduction	Beheler et al. (2003)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Collared flycatcher *Ficedula albicollis*	BDD	Sex, RS, Size, Cond, Den	Adult females dispersed farther than adult males; Both sexes dispersed further after unsuccessful reproduction	Pärt and Gustafsson (1989)
		NDD	Sex, Size, Cond, Den.	Juvenile females dispersed farther than juvenile males; Females from small broods moved farther than females from large broods	Pärt (1990)
		NDD	Pros.	Individuals observed prospecting at the nests of conspecifics settled near the prospected site the following year	Pärt and Doligez (2003)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Willow flycatcher *Empidonax traillii*	SF, NDD, BDD	Age, Sex, RS	No difference in return rate or dispersal distance between adult males and adult females; For females, site fidelity was lower and dispersal longer after unsuccessful reproduction; Site fidelity was lower in juveniles than adults	Sedgwick and Grubb Jr (2004)
	Bicknell's thrush *Catharus bicknelli*	DP	Age	Juveniles were more likely to disperse between breeding populations than adults	Studds et al. (2012)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Gray catbird *Dumatella carolinensis*	SF	Age, Sex, RS	Site fidelity did not differ between adults and juveniles; Site fidelity was higher in males than females; Both sexes were more likely to return after successful reproduction	Darley et al. (1977)
	Great reed warbler *Acrocephalus arundinaceus*	NDD, BDD	Age, Sex	Juveniles dispersed farther than adults; Dispersal distance did not differ between the sexes	Hansson et al. (2002)
		BDD	Sex	Females more likely to immigrate into study population than males	Hansson et al. (2004)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Prairie warbler *Setophaga discolor*	SF	Age, Sex, RS	Site fidelity did not differ between adults and juveniles; Site fidelity was higher in males than females; Females were more likely to return after successful reproduction	Nolan Jr (1966)
	American redstart *Setophaga ruticilla*	SF, NDD, BDD	Age, Sex	Site fidelity was higher in adult males than juvenile males	Holmes and Sherry (1992)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
		SF	Age, Sex, RS	Site fidelity was higher in adult males than juvenile males; Site fidelity was higher in males than females; Females were more likely to return after successful reproduction	Lemon et al. (1996)
		NDD, Dir	Age, HQ	Juvenile redstarts from high-quality winter habitat were more likely to disperse north of their natal site whereas individuals from low-quality habitat were more likely to disperse south; No effect of winter habitat quality was observed for adults	Studds et al. (2008)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Black-throated blue warbler *Setophaga caerulescens*	SF, NDD, BDD	Age, Sex	No difference in site fidelity between ages or sexes	Holmes and Sherry (1992)
	Prothonotary warbler *Protonotaria citrea*	SF	Age, Sex, RS, Par.	Site fidelity increased with the number of broods produced; No effect of age, sex or brood parasitism	Hoover (2003)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Indigo bunting *Passerina cyanea*	SF, DP	Age, Sex, RS	Adults more faithful to breeding sites than younger individuals; Females more likely to disperse than males; First-year males were more likely to disperse following reproductive failure	Payne and Payne (1993)
	Savannah sparrows *Passerculus sandwichensis*	NDD	Sex, Size Den	Natal dispersal distance did not differ between males and females	Wheelwright and Mauck (1998)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
		NDD, BDD	Age, Sex, HQ, RS	Natal dispersal distances were greater than breeding dispersal distances; Habitat quality did not influence natal dispersal or breeding dispersal; Reproductive success did not influence subsequent breeding dispersal	Fajardo et al. (2009)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	White-crowned sparrow *Zonotrichia leucophrys oriantha*	SF, NDD, BDD	Age, Sex, Pros, RS	Site fidelity was higher in juveniles that prospected after fledging than individuals that immediately left their natal area; Site fidelity was higher in males than females; Dispersal distance decreased with age in females but not males; Reproductive success did not influence subsequent dispersal	Morton (1992)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Bobolink *Dolichonyx oryzivorus*	SF, NDD, BDD	Age, Sex, HQ, RS	Individuals from high-quality sites were more likely to return than individuals from low-quality sites as result of differences in reproductive success; Site fidelity higher in males than females; Site fidelity higher in adult females than juvenile females; Both sexes dispersed further following unsuccessful reproduction	Bollinger and Gavin (1989)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
		NDD, BDD	Age, Sex, HQ, RS	Natal dispersal distances were greater than breeding dispersal distances; Habitat quality did not influence natal dispersal but adults were more likely to disperse to high-quality sites; Reproductive success did not influence subsequent breeding dispersal	Fajardo et al. (2009)
Mammals					
	Caribou *Rangifer tarandus caribou*	SF	Age, RS	No evidence for age differences in site fidelity; Number of calves produced did not influence site fidelity in subsequent years	Schaefer et al. (2000)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
		SF	HQ	Individuals did not shift breeding sites in response to petroleum development	Tracz et al. (2010)
	Mule deer *Odocoileus hemionus hemionus*	BDD	Sex	Females dispersed shorter distances between consecutive summer ranges than males	Brown (1992)
	Wildebeest *Connochaetes taurinus*	DP	Sex, RS	No evidence that dispersal probability differed between sexes; Breeding females more likely to disperse than non-breeders	Morrison and Bolger (2012)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Polar bear *Ursus maritimus*	SF	Clim	In years with rapid ice melt on the Hudson Bay, individuals remained on drifting ice floes and were less faithful to denning sites used the previous year	Cherry et al. (2013)
	Manatee *Trichechus manatus*	SF	Age, Sex	No evidence for age or sex differences in breeding site fidelity	Deutsch et al. (2003)
	Sperm whale *Physeter macrocephalus*	GF	Sex	Significant mtDNA differentiation between regions but no differentiation in microsatellite loci, suggesting male-biased gene flow	Lyrholm et al. (1999)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
		GF	Sex	Significant mtDNA differentiation between regional populations while microsatellites showed much less differentiation, suggesting male-biased gene flow	Engelhaupt et al. (2009)
Amphibians					
	Wood frog *Rana sylvatica*	SF, NDD, BDD	Age	Site fidelity to breeding ponds higher in adults than juveniles	Berven and Grudzien (1990)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Marbled salamander *Ambystoma opacum*	SF, NDD, BDD	Age, Den	Site fidelity to breeding ponds higher in adults than juveniles; Dispersers more likely to leave small populations and immigrate into ponds with large populations	Gamble et al. (2007)
	California tiger salamander *Ambystoma californiense*	DP	Age, Den	No evidence for age or sex differences in dispersal probabilities	Trenham et al. (2001)
Reptiles					

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Hawksbill sea turtle *Eretmochelys imbricata*	GF	Sex	Genetic diversity suggests males more likely to disperse to non-natal rookeries than females	Velez-Zuazo et al. (2008)
	Green seas turtle *Chelonia mydas*	GF	Sex	mtDNA markers indicate strong regional population structure but nDNA markers indicate moderate gene flow, suggesting that male-biased dispersal	Karl et al. (1992)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
		GF	Sex	mtDNA haplotype frequencies similar for males and females at the same courting area, suggesting strong site fidelity by both sexes	FitzSimmons et al. (1997)
	Loggerhead sea turtle *Caretta caretta*	SF	Sex	No evidence of sex differences in fidelity to courting areas	Carreras et al. (2007)
Fish					

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Chinook salmon *Oncorhynchus tshawytscha*	DP	Age, HQ	Older individuals more likely to disperse than younger individuals; Presence of volcanic ash increased dispersal probability the following year	Quinn et al. (1991)
		SF	Sex, HQ	Site fidelity higher in females than males; For females, site fidelity higher in patchy habitat than in continuous habitat	Neville et al. (2006)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
		SF	Impr	Individuals released early or late and individuals transported to other streams had lower return rates than individuals released at intermediate dates or in their natal stream	Pascual et al. (1995)
		DP	Age, Sex, Den	Males more likely to disperse to non-natal stream than females; high juvenile movement within natal stream increased probability of adult dispersal	Hamann and Kennedy (2012)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
(b) Non-breeding season					
Birds					
	Black brant *Branta bernicla nigricans*	SF	Sex	No evidence for sex differences in site fidelity	Reed et al. (1998)
	Canada geese *Branta Canadensis*	DP	Clim	Harsh winter increased the probability of dispersal between non-breeding regions	Hestbeck et al. (1991)
	White-fronted geese *Anser albifrons flavirostirs*	DP	Age, Sex	No evidence of sex differences in dispersal probability between wintering sites; Juveniles more likely to disperse than adults	Wilson et al. (1991)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
		SF	Age, Sex, Den	Site fidelity was higher for individuals $>$ 2 yrs old than for younger individuals; no evidence for density-dependent dispersal	Marchi et al. (2010)
	American black duck *Anas rubripes*	SF	Age, Sex, HQ	No evidence of age or sex differences in site fidelity; Predictable food resources in coastal sites led to higher site fidelity than to less predictable inland sites	Diefenbach et al. (1988)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Eurasian spoonbills *Platalea leucorodia* leucorodia	SF, DP	Age	Site fidelity higher in adults than juveniles; juveniles that spent their first winter in Europe more likely to disperse to Africa during their second winter than vice versa	Lok et al. (2011)
	Black-chinned hummingbird *Archilochus alexandri*	SF	Sex	No evidence for sex differences in site fidelity	Bassett and Cubie (2009)
	Rufous hummingbird *Selasphorus rufus*	SF	Sex	Site fidelity higher in females than males	Bassett and Cubie (2009)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Ruby-throated hummingbird *Archilochus colubris*	SF	Sex	Site fidelity higher in females than males	Bassett and Cubie (2009)
	Prairie Warbler *Setophaga discolor*	SF	Age, Sex, HQ	Site fidelity higher in males than females; Site fidelity higher in juveniles than adults	Latta and Faaborg (2001)
		SF	Par	No individuals infected with scaley leg mite (Knemidokoptes jamaicensis) returned the following year	Latta and Grubb (2003)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Palm warbler *Setophaga palmarum*	SF	Par	No individuals infected with scaley leg mite (Knemidokoptes jamaicensis) returned the following year	Latta and Grubb (2003)
	American redstart *Setophaga ruticilla*	SF, DD	Age, Sex	No evidence for age or sex differences in site fidelity	Holmes and Sherry (1992)
	Black-throated blue warbler *Setophaga caerulescens*	SF, DD	Age, Sex	No evidence for age or sex differences in site fidelity	Holmes and Sherry (1992)
Mammals					
	Caribou *Rangifer rarandus caribou*	SF	Age	Site fidelity higher in adult females than juvenile females	Schaefer et al. (2000)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
		SF	HQ	Individuals shifted winter sites in response to the amount of snow cover	Wittmer et al. (2006)
		SF	HQ	Herd avoided winter sites that were heavily used the previous winter	Schmelzer and Otto (2011)
		SF	Clim	Site fidelity to calving grounds was a function of snow cover	Mahoney and Schaefer (2002)
	Moose *Alces alces*	SF	Age, Sex, Den	Fidelity to non-breeding range did not differ between sexes or age classes and was not related to population density	Sweanor and Sandegren (1989)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Mule deer *Odocoileus hemionus hemionus*	DD	Sex, Clim	Dispersal distance between consecutive winter ranges did not differ between males and females; During mild winters, individuals less likely to migrate to normal winter ranges	Brown (1992)
	Manatee *Trichechus manatus*	SF	Age, Sex	No evidence for age or sex differences in site fidelity	Deutsch et al. (2003)
Amphibians					
	Red-nosed stub-footed toad *Atelopus oxyrhynchus*	SF	Sex	No evidence for sex differences in site fidelity	Dole and Durant (1974)
(c) Migration/Stopover					

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
Birds					
	Bluethroat *Luscinia svecica*	SF	Age, Sex	No evidence for age or sex differences in fidelity	Catry et al. (2004)
	Reed warbler *Acrocephalus scirpaceus*	SF	Age, Sex	Site fidelity higher in adults than juveniles	Catry et al. (2004)
(d) Molt					
Birds					

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Dark-bellied brent geese *Branta b. bernicla*	SF	RS	Individuals were more faithful to island molting sites following years with poor reproductive success due to high predation; in years with high reproductive success, adults moved to the mainland to molt and avoid predation on gooslings	Ebbinge et al. (2013)
	Great reed warbler *Acrocephalus arundinaceus*	SF	Age	No evidence for age differences in site fidelity	Yohannes et al. (2007)

Taxon	Species	Measure of Dispersal[1]	Factors Studied[2]	Results	Reference
	Steller's eider *Polysticta stelleri*	SF	Sex	No evidence for sex differences in site fidelity to molting ponds	Flint et al. (2000)
	King eider *Somateria spectabilis*	SF	Sex	Site fidelity to molting locations higher for males than females	Phillips and Powell (2006)
	Paradise shelduck *Tadorna variegata*	SF	Sex	No evidence of sex differences in fidelity to molting sites	Barker et al. (2005)

APPENDIX B: ADDITIONAL FIELD AND LABORATORY METHODS

Field Methods

Starting on April 10th of each year, the site was surveyed every three days from 0600 to 1200 along transects spaced 100m apart to record any male seen or heard. During each survey, the territory boundaries of all males were mapped by following the individual for 10 minutes or until visual contact was lost and recording their approximate locations on a gridded map of the study site. The arrival date of each male was recorded as the first day in the 3-day survey period that it was recorded. Males were captured in mist nets within 7-10 days of arrival using playback of conspecific song and a decoy. Female redstarts are cryptic during the nest building period and do not generally respond to conspecific playback. Therefore females were captured in mists nets while feeding fledglings later in the season.

Stable Isotope Analysis

Feathers and claws were cleaned in 2:1 chloroform:methanol solution and air dried in a fume hood for 48 hours. Samples were transported to the Smithsonian Stable Isotope Mass Spectrometry Laboratory in Suitland, Maryland

where the feathers were allowed to equilibrate with the local atmosphere for $>$ 72 hours. After equilibration, a 0.3-0.4mg sample was clipped from the distal end of each feather and loaded into a silver capsule. For claw samples, 0.3-0.4mg of each sample was loaded into a tin capsule. Samples were then crushed, pyrolized at 1350^{o}C in an elemental analyzer (Thermo TC/EA), and introduced in a continuous-flow isotope ratio mass spectrometer (Thermo Delta V Advantage) via a Conflo IV interface. Calculations of raw isotope values were performed with Isodat 3.0 software. All runs included a set of standards for every 10-12 samples. The stable hydrogen (δ^2H) values reported include only non-exchangeable hydrogen, as determined by a 3-point linear correction using keratin standards [1]. All values are expressed in the typical delta notation in units of per mil (‰) normalized on the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW-SLAP) scale for hydrogen and the Vienna PeeDee Belemnite scale for carbon. Analytical error was better than 2‰ for hydrogen samples and 0.2‰ for carbon samples based on replicate analyses of standards.

Determining dispersal status

We probabilistically determined the origin of all unknown-origin individuals in our population using year-specific distributions of local δ^2H_f values [2]. We first estimated the expected local δ^2H_f value for each year using the mean δ^2H_f values from either breeding adult males (2009) or from individuals known to have bred at the study site the previous year (2010-2012). Next,

we centered the δ^2H_f values from all recaptured individuals from 2010-2012 on the year-specific means and, because the mean-centered values were normally distributed (Shaprio-Wilk test: $W = 0.972$, $P = 0.5123$), we used the standard deviation of these values (7.179‰) as a measure of local variation in δ^2H_f values. Finally, we used the year-specific means and pooled standard deviation to probabilistically assign all unbanded individuals into one of three dispersal categories based on a predefined odds ratio for correctly classifying individuals as local. This odds ratio was used to calculate the range of δ^2H_f values capturing a given area under each year-specific local distribution (e.g. 80%) and individuals with δ^2H_f values within this range were classified as local while individuals with δ^2H_f values more negative or positive than the threshold range were classified as "northern" or "southern," respectively [2]. To test the sensitivity of our results to the threshold used to classify dispersal status, we carried out the classifications using three progressively stringent thresholds (4:1 odds, 9:1 odds and 19:1 odds) and performed all analyses under each scenario.

Previous studies using hydrogen isotopes to determine the origin of songbirds [3, 4] have applied a correction factor to hydrogen values from yearling individuals to account for possible age-specific isotope discrimination. Over the course of our study, we recaptured six yearlings that were originally banded at our study site as nestlings and hydrogen values from these individuals did not differ from the values of recaptured adults individuals (yearling mean = -64.76‰, adult mean = -64.72‰, $t = 0.016$, $df = 5$, P = 0.988). Therefore, we chose not to apply any age-correction to the hydrogen values from unbanded yearlings.

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APPENDIX C: SUPPLEMENTARY RESULTS FOR CHAPTER 3

Results of Dispersal Classifications

	Origin		
	South	Local	North
Yearlings			
2009	3 (10%)	21 (72%)	5 (18%)
2010	0 (0%)	22 (67%)	11 (33%)
2011	1 (2%)	42 (89%)	4 (9%)
2012	3 (6%)	46 (90%)	2 (4%)
Total	**7 (4%)**	**131 (82%)**	**22 (14%)**
Adults			
2009	0 (0%)	65 (97%)	2 (3%)
2010	2 (6%)	29 (91%)	1 (3%)
2011	2 (7%)	23 (74%)	6 (19%)
2012	4 (13%)	25 (83%)	1 (4%)
Total	**8 (8%)**	**142 (89%)**	**10 (6%)**

(a)

	Origin		
	South	Local	North
Yearlings			
2009	2 (7%)	23 (79%)	4 (14%)
2010	0 (0%)	25 (76%)	8 (24%)
2011	0 (0%)	45 (95%)	2 (5%)
2012	2 (4%)	49 (96%)	0 (0%)
Total	**4 (3%)**	**142 (88%)**	**14 (9%)**
Adults			
2009	0 (0%)	66 (98%)	1 (2%)
2010	0 (0%)	31 (97%)	1 (3%)
2011	0 (0%)	27 (84%)	4 (16%)
2012	2 (7%)	28 (93%)	0 (0%)
Total	**2 (1%)**	**152 (95%)**	**6 (4%)**

(b)

	Origin		
	South	Local	North
Yearlings			
2009	1 (4%)	25 (86%)	3 (10%)
2010	0 (0%)	30 (91%)	3 (9%)
2011	0 (0%)	46 (98%)	1 (2%)
2012	1 (2%)	50 (98%)	0 (0%)
Total	**2 (1%)**	**151 (94%)**	**7 (5%)**
Adults			
2009	0 (0%)	66 (98%)	1 (2%)
2010	0 (0%)	31 (97%)	1 (3%)
2011	0 (0%)	29 (94%)	2 (16%)
2012	2 (7%)	28 (93%)	0 (0%)
Total	**2 (1%)**	**154 (96%)**	**4 (3%)**

(c)

Table C1: Summary of dispersal status assignments for American redstarts breeding at the Patuxent Research Refuge from 2009-2012 based on (a) 4:1 odds ratio, (b) 9:1 odds ratio and (c) 19:1 odds ratio. Cells contain the number of individuals assigned to each age class. Origin refers to where breeding occurs relative to overwintering sites where habitat conditions directly influence departure and arrival into breeding habitats. Parentheses indicate the percentage of individuals in each class.

Results of analyses based on 9:1 and 19:1 odds ratios

Table C2: (Next page) Summary of model selection results for dispersal assignments based on (a) 9:1 odds ratio and (b) 19:1 odds ratio. Only models with $\Delta AIC_c < 4$ in the final model suite are shown. Additive effects are indicated by (+). Interactions between two variables are indicated by (x). Significant coefficients (95% CI do not contain zero) are shown in bold. Near significant coefficients (90% CI do not contain zero) are shown in italics.

Model	k	AIC_c	ΔAIC_c	w_i
Age + **Phenology** + **NDVI**	5	199.38	0.00	0.10
Age + **Phenology** + **NDVI** + Condition	6	199.58	0.20	0.09
Phenology + **NDVI**	4	199.68	0.30	0.09
Phenology + **NDVI** + Condition	5	200.16	0.78	0.07
Age + **Phenology** + **NDVI** + **Age** × **Phenology**	6	200.40	1.02	0.06
Age + **Phenology** + **NDVI** + Condition + **Age** × **Phenology**	7	200.62	1.24	0.05
Age + **Phenology** + **NDVI** + Condition + Age × Condition	7	200.78	1.40	0.05
Age + **Phenology** + NDVI + Age × NDVI	6	200.92	1.54	0.05
Age + **Phenology** + NDVI + Condition + Age × NDVI	7	201.10	1.72	0.04
Age + **Phenology** + **NDVI** + $\delta^{13}C$	6	201.44	2.06	0.04
Phenology + **NDVI** + $\delta^{13}C$	5	201.48	2.10	0.03
Age + *Phenology* + NDVI + **Age** × **Phenology** + Age × NDVI	7	201.51	2.13	0.03
Age + **Phenology** + NDVI + Condition + $\delta^{13}C$	7	201.67	2.29	0.03
Age + *Phenology* + NDVI + Condition + **Age** × **Phenology** + Age × NDVI	8	201.69	2.31	0.03
Phenology + **NDVI** + Condition + $\delta^{13}C$	6	202.07	2.69	0.03
Age + **Phenology** + **NDVI** + Condition + **Age** × **Phenology** + Age × Condition	8	202.15	2.77	0.02
Age + **Phenology** + NDVI + Condition + Age x NDVI + Age × Condition	8	202.28	2.90	0.02
Age + **Phenology** + **NDVI** + $\delta^{13}C$ + **Age** × **Phenology**	7	202.48	3.10	0.02
Age + **Phenology**	4	202.59	3.21	0.02
Age + **Phenology** + **NDVI** + Condition + $\delta^{13}C$ + **Age** × **Phenology**	8	202.72	3.34	0.02
Age + **Phenology** + Condition	5	202.75	3.37	0.02
Age + **Phenology** + **NDVI** + Condition + $\delta^{13}C$ + Age × Condition	8	202.87	3.49	0.02
Age + **Phenology** + NDVI + $\delta 13C$ + Age × NDVI	7	202.99	3.61	0.02
Age + *Phenology* + **Age** × **Phenology**	5	203.06	3.68	0.02
Age + **Phenology** + NDVI + Condition + $\delta 13C$ + Age × NDVI	8	202.30	3.82	0.01
Age + *Phenology* + NDVI + Condition + **Age** × **Phenology** + Age × NDVI + Age × Condition	9	203.26	3.88	0.01
Age + *Phenology* + Condition + **Age** × **Phenology**	6	203.26	2.88	0.01

(a)

Model	k	AIC_c	ΔAIC_c	w_i
Phenology	3	136.38	0.00	0.18
Age + **Phenology**	4	136.71	0.33	0.16
Phenology + NDVI	4	137.19	0.81	0.12
Phenology + $\delta^{13}C$	4	137.27	0.89	0.12
Age + **Phenology** + NDVI	5	137.90	1.52	0.09
Phenology + NDVI + $\delta^{13}C$	5	138.19	1.81	0.07
Age + **Phenology** + $\delta^{13}C$	5	138.21	1.83	0.07
Age + **Phenology** + *Age x Phenology*	5	138.71	2.33	0.06
Age + **Phenology** + NDVI + $\delta^{13}C$	6	139.41	3.03	0.04
Age + **Phenology** + NDVI + Age x NDVI	6	139.95	3.58	0.03
Age + **Phenology** + NDVI + *Age x Phenology*	6	139.95	3.58	0.03
Age + **Phenology** + $\delta^{13}C$ + *Age x Phenology*	6	140.25	3.87	0.03

(b)

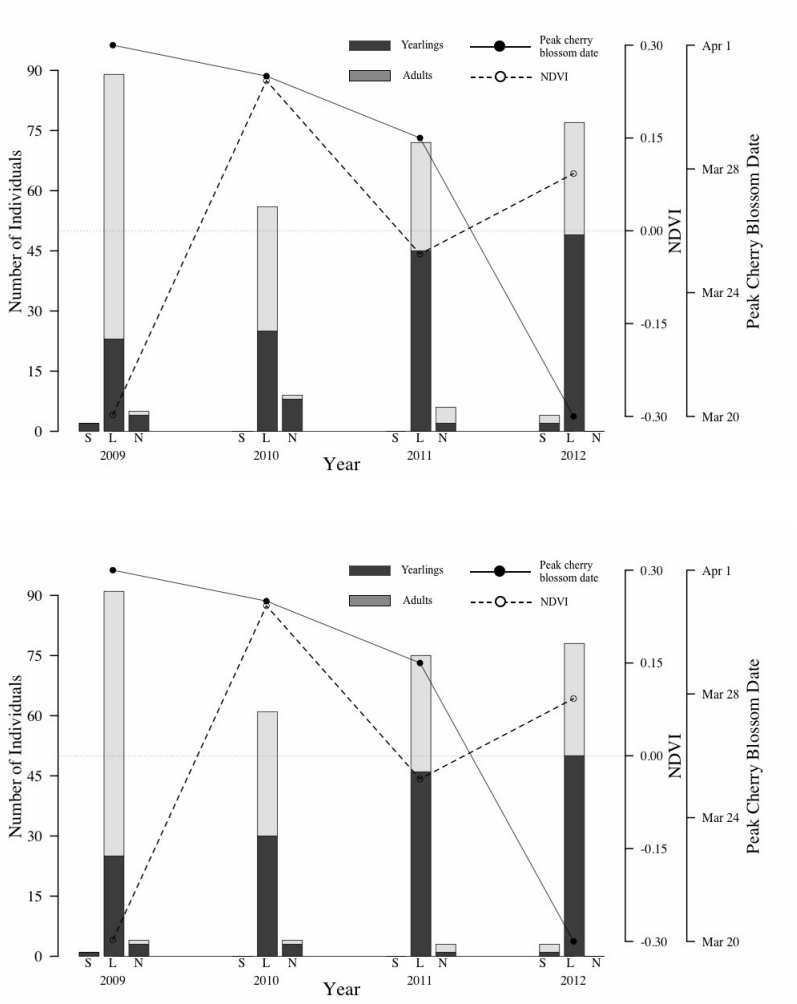


Figure C1: Patterns of immigration into the study population and variation in climate variables from 2009 to 2012. The top panel shows results based on a 9:1 odds ratio for classifying dispersal status and the bottom panel shows results based on using a 19:1 odds ratio. Within each year, the left bar shows the number of individuals with a southern origin ("S"), the center bar shows the number of local individuals ("L"), and the right bar shows the number of individuals with a northern origin ("N"). The solid line and closed circles show the peak cherry blossom date for each year while the dashed line and open circles show the average NDVI value from January to March in Cuba. NDVI values are mean-centered so positive values (above the dotted line) represent above average primary productivity and negative values (below the dotted line) represent below average primary productivity.

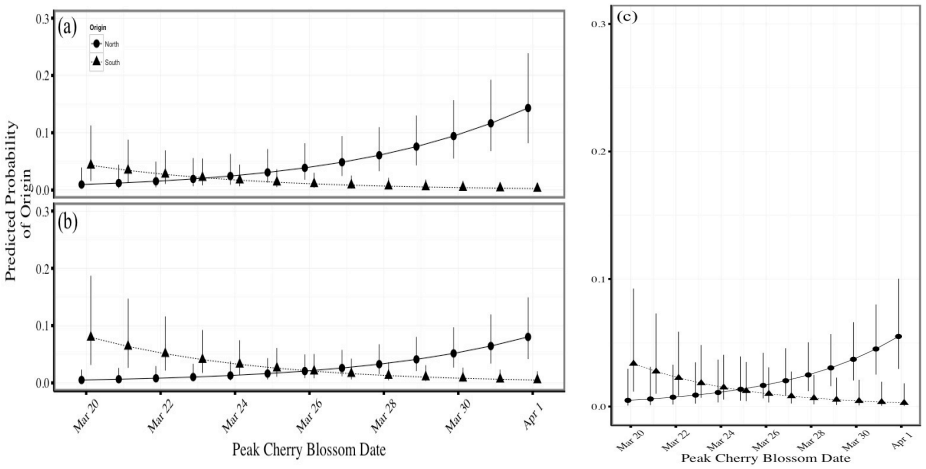


Figure C2: Predicted probability of origin as a function of cherry blossom phenology on the breeding grounds based on the top model for (a) yearlings and (b) adults based on the 9:1 odds ratio and (c) all individuals 19:1 odds ratio candidate sets. The top model in the 19:1 candidate set did not contain the multiplicative effect of NDVI on age class. Triangles and dashed lines show the probability of originating to the south; Circles and solid lines show the probability of originating to the north. Horizontal bars show 95% CI.

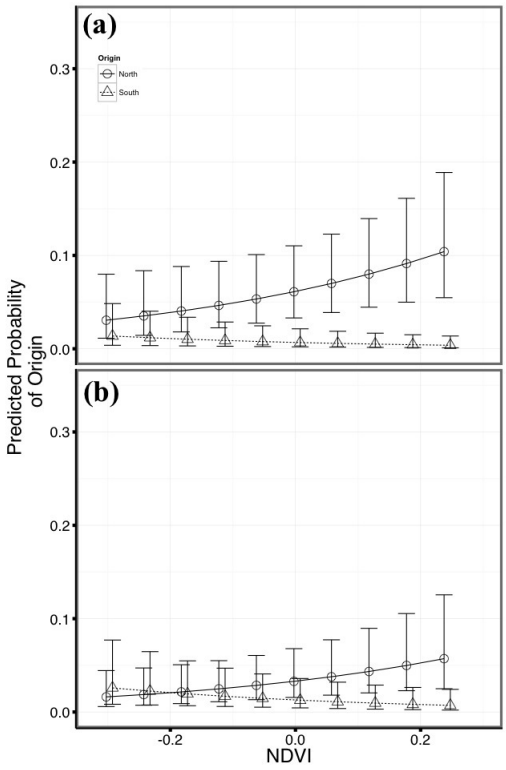


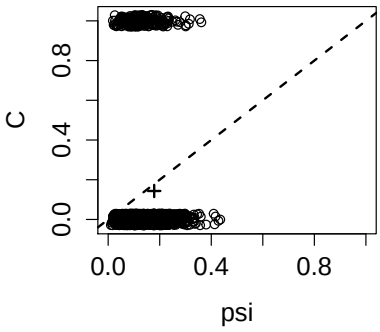
Figure C3: Predicted probability of origin as a function of the Normalized Difference Vegetation Index (NDVI) values from January to March in Cuba based on the top model from the 9:1 odds ratio candidate set for (a) yearlings and (b) adults. NDVI values were mean-centered on the long-term average, thus positive values indicate higher quality conditions and negative values indicate lower quality conditions. Triangles and dashed lines show the probability of originating to the south; Circles and solid lines show the probability of originating to the north. Horizontal bars show 95% CI.

APPENDIX D: SUPPLEMENTARY RESULTS FOR CHAPTER 5

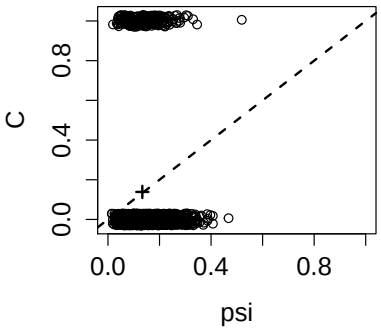
Results of habitat principle component analysis

Habitat Variable	**PC 1**	**PC 2**	**PC 3**
Eigenvalue	1.54	1.35	1.13
Percent of variance explained	33.75	26.16	18.28
Shrub cover	-0.435	0.125	-0.479
Number of saplings	-0.0582	0.439	-0.572
Number of beech trees	0.601	0.0103	-0.0934
Total number of trees	0.579	-0.0745	-0.233
Total basal area	0.143	0.341	-0.343
Mean tree basal area	-0.244	-0.582	-0.425
Percent canopy cover	0.174	-0.574	-0.286

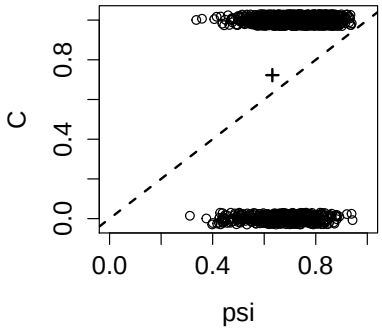
Table D1: Results of principle component analysis of seven habitat variables measured at experimental playback locations. The first three components, shown here, explained over 78% of the variance and were included as covariates in the *settlement* model. Values for habitat variables indicate factor loadings for each component.



(a) Control



(b) Public information



(c) Conspecific attraction

Figure D1: Results of posterior predictive checks for the settlement model. Jittered open circles show simulated settlement data based on draws from the posterior distributions of each parameter. The dashed line shows the expected 1:1 relationship between the probability of settlement (psi) and the proportion of sites that are settled. Cross marks show the mean of the simulated values (y-axis) and the actual proportion of sites that were settled in the experiment (x-axis). Therefore, cross marks close to the 1:1 line indicate good model fit.

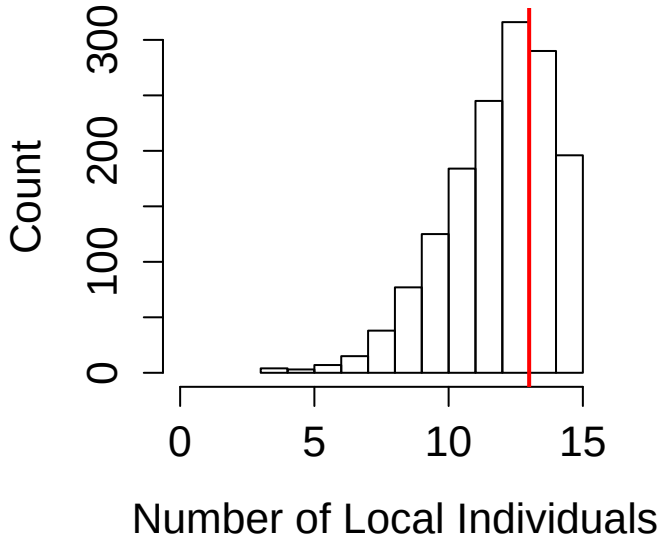


Figure D2: Results of posterior predictive checks for the immigration and models. The histogram shows the simulated number of local individuals based on draws from the posterior distribution for p_{PB} for the 4:1 odds ratio model. The red line shows the observed number of local individuals at experimental conspecific attraction points.

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